1996

The conservation and ecology of the heath lobelia, Lobelia urens L.

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http://hdl.handle.net/10026.1/2429

The conservation and ecology of the heath lobelia, *Lobelia urens* L.

by

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A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences
Faculty of Science

January 1996

The conservation and ecology of the heath lobelia, *Lobelia urens* L.

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ABSTRACT

This programme of research examines the ecology of the threatened perennial *Lobelia urens* L. (the heath lobelia) which reaches the northern limit of its distribution in the southern coastal counties of England. A survey of the historical evidence of the distribution of the species in England is presented. Restricted to such a small area, *L. urens* has always been rare in Britain. The six remaining populations were surveyed to describe the phytosociology of communities containing *L. urens* and the variability of the environmental factors controlling its distribution. *L. urens* is shown to be a member of rough grass-heath communities dominated by *Molinia caerulea* and situated on seasonally waterlogged, moderately acidic, nutrient-poor soils.

Studies of the demography of *L. urens* focused on two extant populations. Experimental research was carried out to support these demographic studies both in the field, on plants grown in a common garden, and under the controlled conditions of the glasshouse and laboratory. This information on the ecology of *L. urens* was used to construct stage-structured population matrices.

Recruitment success in *L. urens* is shown to be very low in Britain and results suggest that this controls the density of British populations. The availability of seed does not regulate the rate of germination. Instead, recruitment of *L. urens* at the northern edge of its range is restricted by its specific habitat requirements, along with low summer temperatures and the short growing season. Establishment from seed is facilitated by micro-habitats that provide high light intensities and, more importantly, protection against soil moisture loss.

Whilst winter disturbance by herbivores is shown to be essential for successful recruitment, adult growth and survival is better in ungrazed communities. However, even the small plants of the grazed areas are very fecund. The seed forms a large persistent bank that embodies a reserve of individuals and genetic variability which offers protection against extinction.

The thesis concludes that the soil moisture status and disturbance regimes at Redlake and Andrew's Wood are limiting the growth rates of the *L. urens* populations. In order to maintain populations, the redirection of drainage water is prescribed to increase the soil moisture status. *L. urens* is suited to intermittent soil disturbance, the timing and intensity of which was shown to be important, whilst the duration between grazes was seen to be less critical. Results suggest that the habitat created by occasional heavy winter grazing of fattening cattle would be very favourable to *L. urens*.

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ADDITIONAL NOTES

The heath lobelia, *Lobelia urens* is referred to throughout as *L. urens*.

Vascular plant names follow Clapham, Tutin & Moore (1987).

Bryophytes names follow Watson (1981).

Statistics were carried out using STATGRAPHICS.

AUTHOR'S DECLARATION

This study was financed with the aid of a studentship from the University of Plymouth. At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

Presentations and conferences attended:

British Ecological Society winter meeting, Exeter 1991.

Linnean Society and Botanical Society of the British Isles conference on translocation and reinstatement of plant species, London March 1993.

British Ecological Society winter meeting, Stirling 1993 (poster presentation: Determinants of fecundity in the heath lobelia).

British Ecological Society winter meeting, Birmingham 1994.

Biological recording in Cornwall and the Isles of Scilly Seminar, Camborne May 1995.

British Ecological Society winter meeting, Sheffield 1995 (oral presentation: Habitat management and population demography of the heath lobelia).

Departmental seminars, February 1993 and February 1996.

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ONE

Introduction

This thesis aims to investigate the ecology and conservation of *Lobelia urens* L. in southern England. The principal objectives are, first, to describe the life cycle and population biology of *L. urens* and; second, to define the specie's interactions with environmental and biotic factors. Such ecological knowledge provides the correct foundation for conservation management plans. A prerequiste of this research is the examination of *L. urens* species biology.

1.1 Species Biology

The relationship between a species and its ecosystem, the species niche, is easier to define, interpret and discuss if something of the basic biology of the species is known.

1.1.1 *Taxonomy*

Family: Campanullaceae
Genus: *Lobelia*
Species: *L. urens*
English common names: the heath lobelia, acrid lobelia

1.1.2 *Morphology* (Brightmore, 1968; Clapham, Tutin & Moore, 1987)

L. urens is a nearly glabrous, perennial, rhizomatous herb. The rhizome develops a number of rosettes through late autumn to early spring. The median number of rosettes is two or three but plants can have as many as twenty (personal observation). The rosette leaves are obovate, sub-petiolate and irregularly dentate. The average rosette is made up of ten to fifteen leaves each of which is 50-100 mm long. Each rosette produces an erect slender spike that grows to

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Plate 1.1: The morphology of *L. urens* (a) large plant in flower at Andrew's Wood, July, 1995, (b) detail of individual flowers, (c) scanning electron micrograph of seed.

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10-100 cm (Plate 1.1a). The spike may be simple or branching with bracts much narrower and shorter than the rosette leaves. The inflorescence is rather lax and typically has forty to eighty purplish-blue flowers between June and October. The flowers are hermaphrodite, zygomorphic, resupinate, pentamerous and entomophilous. The calyx tube is cylindrical, up to 12 mm long and distinctly ribbed with almost linear teeth which are shorter than the tube. The corolla is 10-15 mm long, purplish-blue in colour and bilabiate. The upper lip is bilobed, almost cleft to its base and the lower lip trilobed; all lobes have recurved acute apices (Plate 1.1b). The stamens have free filaments attached to base of the corolla tube. The anthers are black with whitish hairs and shortly exserted, while the two lower anthers are bearded. The style is slender; the stigma capitate and weakly bilobed. The ovary is bicarpellary and inferior with numerous ovules of axile placentation. The capsules are held erect on the stem, they are elliptical [8 x 20 mm], brown in colour and finely striate. A typical capsule contains around 200 seeds, each less than 1 mm in length, light brown and rather shiny (Plate 1.1c). These seeds are dispersed a short distance when the dry capsule dehisces loculicidally by two apical pores. In late autumn, after seed ripening, the flowering spikes die back and new rosettes emerge from the rhizome.

1.1.3 *Medicinal uses of the Lobeliaceae*

The Lobeliaceae have been used as drugs throughout history (Holliday, 1969). Their medicinal properties are due to the latex which contains alkaloids such as lobinaline, lobelanine and lobeline (Mascré & Créte, 1932; Krochinal *et al.*, 1972a). Of these, lobeline has been prescribed most commonly and it is said to resemble nicotine and coniine in its action as a powerful emetic and respiratory stimulant (Edmunds, 1904; MAFF, 1968): it has been used throughout history to induce spasms (Grieve, 1971) and for the treatment of asthma and bronchitis (Howes, 1974). The central pharmacological action of Lobeline today is as an expectorant (Perfitt, managing director of Gerard House, personal communication). All the Lobeliaceae contain the above three alkaloids but *L. inflata* has the highest lobeline content (Krochinal *et al.*, 1970, 1972b) and has been cultivated to increase the yield per plant (Krochinal

et al., 1972b).

1.1.4 *Geographical and altitudinal distribution*

L. urens shows a Lusitanian distribution in Europe and North Africa that extends from Morocco, Madeira and the Azores, in the south, along the Atlantic coast through Portugal, Spain and France as far as Belgium (Forbes, 1846; Brightmore, 1968; Tutin *et al.*, 1976; Daniels, 1990). In the extreme south of Europe *L. urens* is of frequent occurrence in the mountains west of Gibraltar (Wolley-Dod, 1914). In Madeira, the plant is mainly found between 600-915 m (Brightmore, 1968) and in the Azores, where it occurs on the islands of Terceira and Faila, it is found above 300 m in grazed pasture (Sjögren, 1984). Further north, in west Spain, the main locations are in upland valleys, reaching 830 m in the Montes de Toledo and extending to the southwest into the Guadiana valley (Brightmore, 1968). In Portugal it is present in the coastal plain, passing inland up the valleys of the wetter northern provinces to 800 m. *L. urens* is found in the Pyrenees but further north in France it is restricted to lowland coastal areas. *L. urens* reaches its northern distributional limit in Britain and is confined to the southern coastal counties of England: Cornwall, Devon, Dorset, Hampshire, Sussex and Kent, with a single record for a colony in Herefordshire (section 2.2). In Britain it is a lowland species (Wilson, 1949) with an altittudinal range from 25 m in the New Forest to 210 m at Yarner Wood, Devon (section 2.2).

Climate exerts the predominant controls on the world distribution of species (Cain, 1944) and temperature is the major climatic determinant of species distribution (Coope, 1977; Atkinson *et al.*, 1987). The physiological mechanisms by which temperature operates on species distributions are incompletely understood (Grace, 1987). Plants have a optimum temperature for growth and also absolute temperature limits to survival (Wilson, 1949; Grace, 1987; Beerling, 1993). Brightmore (1968) interpreted the 5°C January isotherm as the lower temperature limit for *L. urens* but such hard two dimensional temperature limits are improbable (Jeffree & Jeffree,

1994): first, because individuals are not genetically identical and show phenotypic variation in their tolerance of temperature; and second, because response to low winter temperature is affected by the preceding summer temperatures and consequently shows variation with geographic location (Jeffree & Jeffree, 1994). Furthermore, the edaphic environment must be given full consideration, since sandy soils and soils over free-draining baserock, such as limestone or chalk, are more easily warmed than those of a contrary character such as clay. In porous soils, plants may attain a higher altitude or a more northerly distribution than in soils which are heavy, wet and cold (Wilson, 1949). Throughout its range, *L. urens* is found in infertile, siliceous acid soils (Brightmore, 1968). At its northern limit, these soils are mainly argillic and lie over more clayey horizons. As a result, they are badly drained areas that are waterlogged for at least part of the year and this can intensify the effects of low temperatures.

L. urens is rare in Britain and is listed in the British red data book (Perring and Farrell, 1977). The species has a clumped distribution, with records for only nineteen sites, yet populations are represented by many individuals where they are found. Although species populations are usually more fragmented towards their distributional limits (Griggs, 1914; Hengevelt & Haeck, 1982; Carter & Prince, 1987), it is not known how *L. urens* dispersed to these disjunct sites, leaving no intermediate occurrences. There are however many, more mysterious, examples of disjunct plant distribution such as how a single tree of the whitty pear (*Sorbus domestica*) got into a remote spot in Wyre forest, Worcestershire at some time before 1600, when its nearest locality was in Brittany (Pitt, 1678)? Or how *Juncus planifolius* came to be known from the South Pacific, Hawaii and one particular remote lough in western Ireland (Scannell, 1973)?

1.2 Conservation

Landscapes without human disturbance epitomise naturalness, yet under this criterion there is nothing even near natural left in Britain. What is seen as nature conservation here in Britain is really aesthetic historic conservation (Rackham, 1980). The historic records of different ages of

human disturbance give Britain's landscapes diversity, not merely genetic diversity, but habitat diversity offering relief in an homogeneous world of concrete and monospecific crops. Leopold (1949) first introduced the concept that all species including *Homo sapiens* are equal and started the movement away from anthropocentric conservation. People can make their mark on the landscape, just as oak trees make theirs, and that landscape will still be natural. The division between the effects of humans and those of other species is that the ever increasing requirements of the growing human populations threaten the majority of plant and animal communities. It is this difference that advocates conservation. Areas chosen to be protected from human exploitation need to be conserved carefully; frequently they cannot be preserved with no further interference, as they are restricted to small isolated patches, where they do not function naturally.

The conservation of rare or endangered species is important, not only as a part of this overall plan to maintain an aesthetically enriched environment, but also because it provides essential opportunities for developing methodologies for effective environmental planning and management on a small scale, that may then form the basis of community or ecosystem conservation.

The 1947 Report of the Wildlife Conservation Special Committee 'Conservation of Nature in England and Wales' called for population studies be undertaken on rare plants. The need for such studies is continually reiterated (Perring & Farrell, 1977; Baskin & Baskin, 1978; Bradshaw & Doody, 1978; White & Bratton, 1981; Harvey, 1985; Palmer, 1987; Lesica, 1992; Primack, 1993), yet to date, there have been few examples of such research (Given, 1994 but exceptions include Meredith, 1978; Wells, 1981; Zhang, 1983; Bullard *et al.*, 1987; Hutchings, 1987a; b; Mehrhoff, 1989; Charron & Gagnon, 1991; Lesica, 1992). This paucity of research is largely because of the enormous investment of time needed to monitor the demography of a rare plant (Davy & Jefferies, 1981; Hutchings, 1990).

L. urens is of particular interest, since it lives up to people's expectations of a rare species. It is elegant and, where it persists, it is very conspicuous in flower, giving a purplish haze to the pastures. Little is known about the status of *L. urens* in continental Europe. Further weighting will be added to its value if it is rare on the continent or if the British populations are shown to be genetically distinct from those of Europe.

1.2.1 *Ecology as the basis for conservation*

At the core of conservation is the science of ecology (Dansereau, 1970). The successful conservation or restoration of a rare species relies on fundamental autecological knowledge (Baskin & Baskin, 1978; Soberón, 1992), which requires rigorous ecological investigation into the species' habitat requirements, life history, population viability, evolution and genetic traits (Warren & Goldsmith, 1974; Gilpin & Soulé, 1986; Lande, 1988; Menges, 1991). The history of a species, the composition of its associated communities and its principal relationships with environmental variables form part of the ground work for autecological studies (Sheail, 1974; 1980; White & Bratton, 1981; Kent & Coker, 1992). However, demographic monitoring is the key to understanding the ecology of all plant species (Harper, 1977; Menges, 1986; Hutchings, 1990; Owen & Rosentreter, 1992; Primack, 1993; Given, 1994; Pavlik, 1994). When demographic monitoring is incorporated into a field experiment, existing habitat conditions or management techniques can be evaluated, and alternative techniques can be designed to hasten population recovery (Harvey, 1985; Menges, 1986; Pavlik, 1994). Unfortunately, for many rare plants, much of this information is lacking when conservation plans are considered (De Mauro, 1994; Pavlik, 1994). As a result, the plans are often standardised, and the recommended research and management actions are too broad or are unrelated to immediate population survival (Cook & Dixon, 1986). This thesis aims to use ecological theory in the formation of cogent management plans for the conservation of *L. urens*.

1.3 Thesis aims

The first objective of this research is to determine the status of *L. urens* in Britain: it is known to be rare and threatened (Perring & Farrell, 1977) but what is its present day distribution and to what extent is it endangered? The study aims to detail information on the life cycle and population biology of *L. urens*, and its relationship with environmental and biotic factors, in order to understand the ecology of *L. urens* at both the community and population level.

The basic philosophy behind the thesis is that factors operate during the life cycle of *L. urens* to regulate the performance of the British populations and thus cause the plant's rarity (Sagar & Mortimer, 1976). The ultimate objectives are to complete a transition matrix for *L. urens* using demographic data, which will reveal the present growth rates of the populations studies and to use elasticity analyses to divulge the life history phases or interphases which restrict population growth (Manders, 1987; Caswell, 1989; Crawley, 1990). Monitoring of areas under different grazing regimes and contrasting these with ungrazed control plots allows an evaluation of grazing management (Palmer, 1987; Pavlik & Barbour, 1993). Such ecological knowledge provides a firm basis for optimal conservation management plans for sites (Darwin, 1872; Zhang, 1983) and thus is the key to protecting and managing a rare species (Primack, 1993; Bowles & Whelan, 1994). The final goal is to prescribe management plans for two *L. urens* sites that will incorporate means of improving this species' status in southern England.

Historical ecology and biogeography

2.1 Introduction

The conservation of rare plant species requires an investigation into their biogeography including the distribution of the species, limiting environmental factors and the impact of human activity both past and present. It has been argued that historical evidence should be disregarded in ecological studies, since individual events can never be fully verified and the history of a site or species is invariably incomplete (see Sheail, 1974; 1980). However, this is a short sighted view, because the history of a species is fundamental in determining its present-day ecology (Sheail, 1974; 1980). Prior to the work described here, the most complete record of the status of *L. urens* in Britain was provided by Perring & Walters (1982) who listed twelve sites at which *L. urens* had been recorded (Figure 2.1). Today, historical records have been found for nineteen sites and plants occur at only six (Figure 2.2). This contemporary account of the historical ecology of *L. urens* in Britain is still fragmentary but forms a very important foundation for the study of the species' requirements.

Species populations are usually more fragmented towards their distributional limits (Griggs, 1914; Hengevelt & Haeck, 1982; Carter & Prince, 1987) and are particularly susceptible to extinction here. In Britain, the remaining *L. urens* populations are clearly fragmented and half are small, with less than 100 plants. Small populations are at risk from demographic stochasticity, genetic drift and inbreeding depression, all of which are exaggerated by habitat and population fragmentation (Franklin, 1980; Soulé, 1985; 1987; Burgman *et al.*, 1993; Bowles & Whelan, 1994; Caughley & Sinclair, 1994).

The biogeography of a species should also form a part of the ground work for autecological
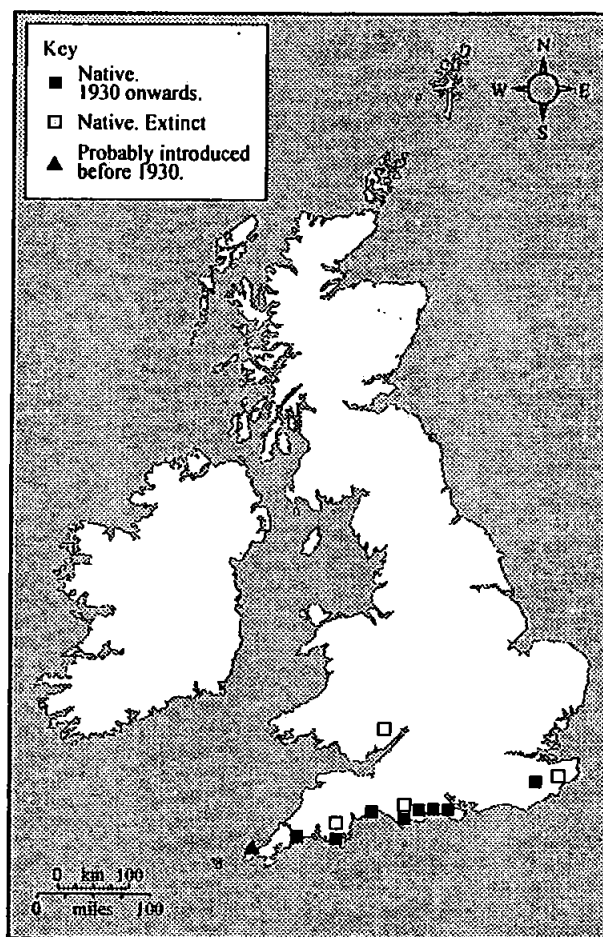
Figure 2.1: The status of *L. urens* in Britain according to Perring and Walters (1982).
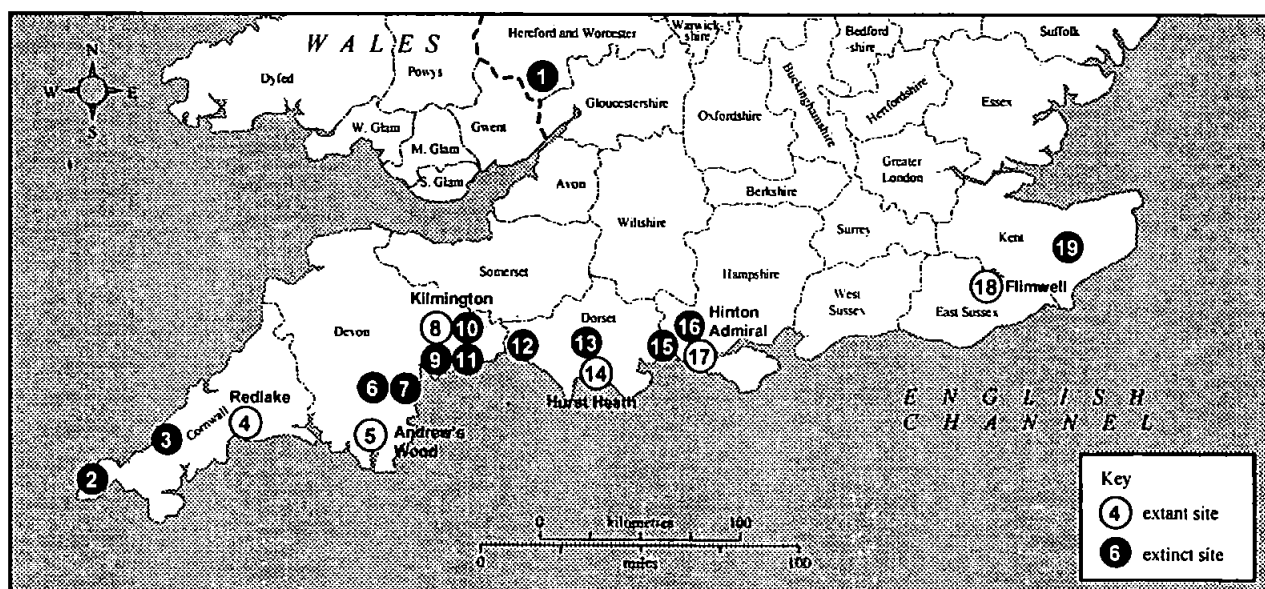
Figure 2.2: The past and present distribution of *L. urens* in southern Britain based on documentary and archive sources and present-day survey.

studies. The understanding of the ecology of a plant community requires a description of the floristics, how the community evolved and its principal relationships with environmental variables (Sheail, 1974; Kent & Coker, 1992). However, single species studies do not generally include research into the characters and composition of associated communities. These details must provide a valuable insight into the species ecology, particularly for rare or threatened species, as the plant's community specificity and the specificity of the community's environmental requirements are major determinants of the species vulnerability to extinction.

There are three aims to this chapter:

(i) to review the historical records and present-day distribution and abundance of *L. urens* in southern England, to determine the status of the species over the past 200 years, the causes of its rarity and its potential to be endangered or threatened;

(ii) to investigate the floristic composition of the plant communities within which the extant *L. urens* populations survive;

(iii) to assess the relative importance of environmental factors in controlling the composition and distribution of communities containing *L. urens*.

2.2 Historical ecology

The aim of this section is to present the documentary evidence for the past and present distribution of *L. urens* in southern England.

Historical records exist for 19 sites in the south but nowhere else in England (Figures 2.1 & 2.2). For the six extant sites, a summary of their recent history and population numbers of *L. urens* is presented in Table 2.1. The information available on both the extinct and extant populations is as follows:

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2.2.1 *Cornwall and Devon*

Historically the British *L. urens* populations have been concentrated in Devon and Cornwall and eleven of the nineteen sites containing *L. urens* in southern England are located in these two counties. The earliest record is from Axminster in east Devon and reads:

"Supra Shute Common inter Axminster et Honiton. D. Newbury," (Clarke, 1778). Also, Andrew's Wood in south Devon, contains the largest extant population.

Populations at eight of the eleven sites are now extinct; one was an unsuccessful introduction and three were lost due to afforestation. The cause of species loss from the other four sites is unknown. The three extant populations are indigenous and two are within designated local nature reserves.

Extinct sites (Figures 2.1 and 2.2)

Near Penzance, Cornwall

L. urens was recorded at this site on a single occasion (Tempère, 1876). No habitat information was presented and Davey (1909) believed that the identification was a mistake.

Ventongimps Moor, Cornwall

In 1968, nine plants were introduced from the population at Redlake, Cornwall under the supervision of J.F. Archibald. It is not known how long they persisted or exactly when they became extinct.

Yarner Wood, Devon

L. urens was first recorded here, amongst stunted oaks and bilberry, by Rev. Keeble Martin (Martin & Fraser, 1901). The population thrived from 1901 to 1913 (Keeble Martin, unpublished) but it had vanished by 1920. *L. urens* reappeared at Yarner Wood, Devon in 1958, after an acre of woodland was cleared for replanting. In 1959, there were 34 plants, but by 1963, there were only four and one or two persisted until 1969. In an unsuccessful attempt

to encourage germination from the seed bank, the trees and ground layer were removed around the former locations of *L. urens* in 1980.

Little Bradley, Devon

In 1981, Dr. B. Merritt recorded *L. urens* in the marshy area of a local nature reserve at Little Bradley near Bovey Tracy, Devon. This is the only record. The close proximity of this site to the former Yarner Wood population (Figure 2.2) makes natural colonisation a distinct possibility but there is also a chance that seed was carried on the boots of conservationists from Andrew's Wood, Devon, since both sites are reserves managed by the Devon Wildlife Trust.

Shute Common 1, Devon

The birch woodland on Shute Common, in which *L. urens* thrived throughout the nineteenth century, was felled in 1960-2 and this site was replanted with Western Hemlock (*Tsuga heterophylla*), bordered with amenity plantings of various hardwood species. The *L. urens* population was greatly reduced by this change in land use: 41 plants were recorded in 1963, declining to 24 in 1967, seven in 1969 and only one in 1990 (Tucker, unpublished). *L. urens* may be surviving in small numbers in the border, where the light intensity is higher but no plants were seen in the present survey.

Shute Common 2, Devon

L. urens flourished beneath birch, probably appearing in the small clearings resulting from natural tree fall. The woodland was felled in 1960-2 and this area was replanted with douglas fir (*Pseudotsuga menziesii*) and hybrid larch (*Larix x. eurolepis*). The population suffered dramatically from this change in land use. Until 1965, 50-60 plants survived but no plants have since been recorded in the plantation.

Field to the north of the A35, Kilmington, Devon

Mr. W. Tucker counted approximately 100 plants in a field here in 1964 and a few remained

until 1969. No plants were found in the present survey, although the habitat is assumed to remain unchanged.

Branscombe, Devon

Dr. Stansfield of the British Pteridophyte society saw *L. urens* on the outskirts of Branscombe in the early 1930s. An attempt by the British Pteridophyte society to relocate the population in 1937 was unsuccessful (Cranfield & Stansfield, 1937).

Extant sites (Figures 2.1 and 2.2; Table 2.1)

Redlake, Cornwall

Webb (1879) suggested that *L. urens* was not to be found in Cornwall. However, Briggs (1883) was told that the plant had been gathered by a Miss Woods on a moor between Lostwithiel and St.Veeps in 1878. In 1883, Mr. Briggs set out to locate this site. He wrote:

> "Hitherto considered to grow in the United Kingdom in the county of Devon only...I found the *L. urens* in two places, a couple of miles apart...One of the stations, an enclosed, though unbroken, rough pasture of about five acres, with a stiff clayey soil, producing short grass and sedge, with *Salnoid succisa* and patches of furze and some heath. Here were dozens of specimens still in flower...probably hundreds over a considerable area,...many cropped by cattle... The other station is a small enclosure of about an acre consisting partly of undrained bog with *Menyanthes, Juncus acutifolia, Molinia* etc. Here it occurs for ten to fifteen yards by a small lushy ridge near the bog and also on the damp lower portion of the hedge-bank, but altogether appears only sparingly. It is associated with *Aquilegia, Hypericum undulatum, Viola lactea, Hydrocotyle, Serratula, Bartsia viscosa, Salix repens,* and a few bushes of *Myrica* with brambles and furze (Briggs, 1883, p359).

During the late 1920s and early 1930s, *L. urens* was recorded from a number of different sites in the St.Veeps/Lerryn/Lostwithiel area, largely by W. Magor. Apart from Redlake Cottage Meadows, all sites have since been taken into agriculture (Jenkins *et al.*, 1984).

Redlake Cottage Meadows was originally used for the rough grazing of ponies and cattle but unfortunately there are few records available regarding the number of plants at Redlake at that time. The first counts in the early 1960s only recorded a handful of plants, but since the 1970s, records generally show numbers to be within the range of 100-200 plants. In 1984, numbers rose to over 1200, which may be connected with management by the Cornish Trust for Nature

Year	Redlake, Cornwall.		Andrew's Wood, Devon.		Kilmington, Devon.	
	Count	Location and management details	Count	Location and management details	Count	Location and management details
1963					30-40	Scattered along upper boundary of a steep sloping unimproved meadow bordering a conifer plantation.
1964	20-30				30-40	
1965	ca.12				40	
1966	100+				16	
1967					18	
1968	250		760		22	
1969					17	
1972	60-70		220			
1973			169			
1974			257	Bullocks broke into reserve mid-summer, cattle in over winter.		
1975			2560	Large increase in compartment C.		
1976			4897			
1977			5325			
1978	180	*L. urens* mainly in field 6 and 7.	2315			
1979	138	ditto.	3915	Increase due to inclusion of new field to reserve (D) which contained large numbers of *L. urens*.		
1980			3970			
1981			3028			
1982			5602	Increase in compartment D.		
1983	137	*L. urens* mostly in north of field 6. Commencement of management by CTNC.	5696	Increase in D and A.		
1984	1221	*L. urens* largely in fields 4 and 6, thriving in trampled areas.	2965	Decline in D but increase in A.		
1985	745	*L. urens* largely in fields 6, fewer in 1, 4, and 7, thriving in trampled areas.	2191			
1986	265	*L. urens* in fields 6, 7 and 4. 2 horses in March, many visitors in summer, 20 cattle in September. Plants not in heaviest poached areas.	2144			
1987	507	Majority of *L. urens* in field 6, small populations in 7 and 4.	842	Low count since no record for D this year.	18	
1988	572		1520	Decline in D but increase in A.		
1989	612		3183	Large increase in D.		
1990	544		5308	Large increase in D.		
1991	221		4948			
1992	207	*L. urens* largely in fields 6 and 7, small population in 4.	3772			
1993	197	4 Exmoor ponies put onto site over winter.	2637	Mainly due to decline in D.	24	In very similar position to first count.
1994	142		4217	Large increase in D.		

Table 2.1: Summary of population numbers and the recent history of *L. urens*. at the six extant sites in southern England.

Year	Hurst Heath, Dorset.		Hinton Admiral, Hampshire.		Flimwell, Sussex	
	Count	Location and management details	Count	Location and management details	Count	Location and management details
1945	1	On edge of remnant heathland.				
1946					few	Thinly scattered on the edges of rides within chestnut coppice.
1952					few	ditto.
1956			12	Cat Plantation, amongst conifers.		
1957	4-5	Between tussocks of long grass.				
1959					few	ditto
1961			8	ditto.		
1965	5		ca.150	Fire in Cat Plantation.		
1967	80	Along belt, 15 metres wide, cleared for drain restoration.	100+	Bracken beginning to smother plants.		
1968	ca.150	ditto.				
1970			ca.100	No plants in plantation, new site in heathy pasture.		
1971					70-80	Confined to rides, chestnuts 5-10 years old
1973	1629	In 'gardened' area.	ca.300	Majority in north-east corner of pasture.		
1974	2101	ditto.			44	Confined to rides.
1976						
1977			27	Pasture now divided into 2, southern half grazed, 10 L. urens Northern half not, 17 L. urens.		
1978			43	All in 1 clump on north-east edge of pasture adjoining plantation.		
1980			26	7 on north-east edge, 11 in newly cut ditch along fence, 8 in ungrazed northern half.		
1981			18	Mostly along ditch.		
1982			8	In northern section of pasture.		
1983			3		5	
1985			60		0	
1986			264	57 in now ungrazed southern half, almost all along wheel ruts 3 in northern section.	200	Trees felled. L. urens widespread through wood.
1988			ca.250			
1990						Site developed as a bird park.
1991			ca.120			
1993			114	In southern section, almost all in ditch.	ca.2500	Scattered throughout bird park.
1994	similar to '74	Still almost all contained within 'gardened' area.				

Table 2.1 (continued): Summary of population numbers and the recent history of *L. urens*. at the six extant sites in southern England.

Conservation (now the Cornwall Wildlife Trust) which began in 1983. Since 1983, there have been annual counts of the numbers of plants in each field within the reserve. The majority of the population has always been in one field in particular, mainly within the heavily poached areas, with fewer plants in the other fields. There has been little grazing between 1986 and 1993, and numbers have declined steadily since the mid 1980s (Table 2.1).

Andrew's Wood, Devon

Capt. Harris-Wise first recorded *L. urens* on Stanton Moor in 1889 over a large expanse of heathy meadow (Martin & Fraser, 1901). In 1894 Sir H. Low recorded 50-80 plants in open places amongst gorse bushes (Martin & Fraser, 1901). The vast majority of this rough ground remained unimproved until the 1950s and the fields lying to the south and east of what is now Andrew's Wood reserve maintained large numbers of *L. urens* (Archibald, 1971). These fields were drained and ploughed after the Second World War for use as arable or ley, leaving Andrew's Wood as a last refuge for *L. urens*.

The wood was declared a Site of Special Scientific Interest (SSSI) in 1952 and has been a reserve since it was leased to the Devon Trust for Nature Conservation (now the Devon Wildlife Trust) in 1965. The Friends of Andrew's Wood, a group of local volunteers with interests in the wood and its natural history, managed the site from that time until 1988, when the Devon Wildlife Trust took over the running of the reserve, having purchased it in 1986. Up until 1965, the reserve was grazed regularly, but since then, grazing has been sporadic and there has been annual cutting to control the scrub invasion. There are few available records regarding plant numbers until 1965 but subsequent annual records, which detail the number of *L. urens* plants in each of the three large clearings on the reserve (Table 2.1), show a great variation in population numbers. The field that probably always contained the most *L. urens* was not part of the reserve until 1979, which makes overall counts before this date appear artificially low. Population numbers still range between 1500 and 5500 plants.

Lobelia Cottage, Kilmington, Devon

Lobelia Cottage is the remaining extant population of the four originally recorded in the locality of Kilmington Hill/Shute Common (Figure 2.2). The first British record of *L. urens* was from this area (Clarke, 1778) and over a hundred years passed before the plant was recorded elsewhere in the country, during which time several accounts of the Shute common populations were written (Withering, 1787; 1796 in Edwards, 1862). Plants were seen in the area by Mrs. M. Bolitho in 1954 but records of the number of plants are only available for the 1960s, when J.F. Archibald visited annually and for the present survey in 1993. These scanty records show that the population has remained small at less than 50 plants and in almost the exact same spot for forty years (Table 2.1).

2.2.2 Dorset and Hampshire

There were four sites of *L. urens* in Dorset and one in Hampshire. Three of the Dorset sites have been lost, two as a result of cultivation. The populations at the two extant sites in both counties are indigenous. They are both privately owned, though one is designated a wildlife advisory site managed by the Dorset Wildlife Trust.

Extinct sites (Figures 2.1 and 2.2)

Puddletown, Dorset

There is a single record of a population here, without an exact location (Lawn, 1956). Cultivation led to the extinction of the population some time before 1965 (Archibald, unpublished).

Morden, Dorset

L. urens was recorded here by Sir H.C. Hawley in 1920 on a grassy heath. By 1965, the site had been cultivated and the population was extinct (Archibald, unpublished).

Lytchett Matravers, Dorset

L. urens was also first reported here by Hawley (1920) and was seen to be flourishing between 1939 and 1945 (The Lord Rochley, personal communication). In 1965, Archibald saw six or seven plants in flower in a small woodland glade. The population was extinct by 1988 (Fitzgerald & Everett, 1989).

Extant sites (Figures 2.1 and 2.2; Table 2.1)

Hurst Heath, Moreton, Dorset

The first report of *L. urens* at Hurst Heath was an uncertain record of a single plant in 1945 (Good, 1945). In subsequent years, plants were occasionally found here at the edge of remnant heathland. The heath borders climax woodland community, with *Pinus sylvestris* and *Betula pubescens* as co-dominants. There are still some poplars standing which were planted in 1880, although part of the wood was burnt in a fire in 1949-50. Adjacent is an arable field which was tile-drained in 1861. In 1957, Dr. J. Hasler saw only four or five specimens in between tussocks of long grass (Good, 1945). In the early 1960s, part of the original drainage system became blocked and during restoration, the vegetation was cleared from a 15 m wide strip, running east-west across the heath. This disturbance lead to a flush of plants from the seed bank (Table 2.1).

Although the land is still privately owned, Hurst Heath became a Dorset Trust for Nature Conservation Wildlife Advisory Site in 1972. Since then, a survey of both seedlings and established plants has been performed annually by volunteers using a grid system to divide up the 480 m^2 site into 120, 2 x 2 m squares.

Initially, work was purely observational but the continual decline in numbers motivated the volunteer group to experiment with management techniques. In 1981, an area was treated with herbicide and in 1986 a 240 m^2 patch, representing half the site, was rotovated. Both treatment plots had significantly more plants than the controls (Bates, 1992). On the basis of these

results, the decision was taken to rotovate a quarter of the area every fourth year. Plots of 120 m^2 were disturbed in 1991 and 1993. This rotationally 'disturbed' area constantly maintains a large population size (Table 2.1).

A sub-population of *L. urens* was found less than a mile away from Hurst Heath by Mr. P. Wilson in 1970. In 1972 there were 110 plants but in 1973 there were 31 and by 1974 only two remained. The field was then cultivated, but in 1978, plants were located in a ditch between the field and a strip of woodland bordering the road. At the time, cattle had access to the area and were seen to trample into the ditch. Mrs. G. Hobson counted 742 plants in 1980 but in the 1993 survey no individuals were found and the hedge was very overgrown with brambles.

Hinton Admiral, Hampshire

Mr J. Vorse was the first to record *L. urens* here, the only population in the county:

> "In July 1903 or '04 a school girl had a bunch of wild flowers. When asking her to name as many as she could, I was astonished to see she had a sprig of *L. urens*. She showed me where it had grown. There were perhaps five or six plants in a little clump or patch, in an opening amongst the firs. Subsequently in the same year I found a few more plants perhaps fifty yards away from the first lot. From these have sprung the many hundreds of plants which now fill the wood" (Linton, 1919 in Archibald, unpublished).

At the time, the site was described as a piece of heathy woodland (Rayner, 1929) but it was replanted with *Pinus sylvestris* in 1949. Several records, each of a handful of plants, exist from the 1950s. In 1965, the plantation was destroyed by fire and this disturbance led to a flush of *L. urens* (Table 2.1) on the cleared ground and amongst the charred pines, especially associated with dense beds of *Teucrium scorodonia* on a fine grass carpet of *Agrostis canina, A. setacea (curtisii)* with *Carex pilulifera*, (Bowman, unpublished).

By 1970, the community within the plantation had recovered and *L. urens* was lost from here. Simultaneously the plant appeared to the south of the plantation in a small area of heathy pasture. The population has been confined to the pasture since then, with plants appearing

largely along ditches or wheel ruts. The larger population numbers coincide with years when three or four clumps of *L. urens* appeared around the pasture and in less successful years *L. urens* was restricted to one cluster (Table 2.1).

2.2.3 *Sussex and Kent*

One extant site remains in Sussex and records exist for at least one site in Kent. These counties are well-known as outposts of the Atlantic species. *L. urens* is one of a group of Lusitanian plants found in the Weald of Sussex and Kent that includes *Hymenophyllum tunbrigense, Ranunculus tripartitus, Lotus angustissimus* and *Sibthorpia europaea.*

Extinct sites (Figures 2.1 and 2.2)

Ashford, Kent

> "Living specimen...presented...Rev. J. Dix of Charing. Found by Mrs. Dix in a wood near Ashford on 27 August last - usually supposed to be a Devon plant, and therefore its discovery in Kent is certainly worthy of record. Mr. Dix informs me that the plant grew about a yard from the path, in a chestnut wood which had been cut down, that it was in full vigour, and that its centre formed a superb spike of flowers. He added that there is no apparent possibility of its having been placed there by man's instrumentality," (Thompson, 1850, p1051).

More recent writers believe that *L. urens* was introduced to the site (Hanbury & Marshall, 1899; Philp, 1982). However, the habitat in the area is very similar to that of the Flimwell colony in Sussex, thirty kilometres away in the Weald, where damp ghyll woodlands create a locally oceanic climate. There seems no reason to doubt the records of this Ashford population and it is possible that *L. urens* may occur at other similar sites in the region. An interesting letter among *The Atlas of British Flora* correspondence in Maidstone refers to an unconfirmed record for Penshurst. The writer says:

> "I fear with the drought it may not have flowered this year (1976)...Lady Hardinge (who identified the plant) is quite a knowledgeable botanist who used to go out with Dr. Druce, so I think it must be a genuine record"

Unfortunately Lady Hardinge died in 1979 and the site has never been identified (Fitzgerald & Everett, 1989).

Extant site (Figures 1 and 2; Table 2.1)

Flimwell, Sussex

L. urens was first noticed here in 1922 by Mrs. E.E. Johnston (Wolley-Dod, 1970) amongst *Castanea sativa*, which was under rotational coppice. The combination of this geographically unexpected location and its late discovery might suggest an introduction but Wilmott (1925) saw no reason to doubt its natural origin. The species must have been well-established when first noticed by Mrs Johnston, since she comments on the annual fluctuations of the population with the weather (Hall, 1980). The population also fluctuated in response to the coppice cycle, surviving along the rides when the trees were mature and then flourishing after they were felled (Table 2.1). In 1990, the site was developed as a bird park. The construction of pens, ponds and paths created large scale disturbance which is perpetuated by bird grazing and visitor trampling. In 1993, upwards of 2500 plants were to be seen scattered throughout the bird park (Table 2.1).

2.2.4 Herefordshire

All the British *L. urens* populations are found along the south coast of England with the exception of a single record for a population in Herefordshire which is now extinct.

Extinct site (Figures 2.1 and 2.2)

Llanrothal, Herefordshire

L. urens was discovered at Llanrothal by Mrs. P. Wiseman (Hyde, 1936). The site was described as:

> "a neglected heathy pasture at about 300 ft altitude, on a moderate slope facing west. The vegetation consisted of *Festuca ovina*, and *Rubus* sp., together with *Juncus* 'communis', *Calluna vulgaris*, *Teucrium scorodonia*, and other species including seedlings of *Crataegus monogyna* and *Acer pseudoplatanus*. I saw

perhaps a dozen plants of the *L. urens* scattered in small groups over an area of
about an acre. The tallest plant was about one foot high: some heads appeared
to be grazed. The locality was in a thinly populated rural district well off the
nearest road (a narrow country lane), and quite away from houses," (Hyde,
1936, p354).

Hyde suggested that the species occurrence was natural, although he pointed out that this new

site represented a greater discontinuity in the distribution of the species in southern England

(Figure 2.2).

The area was searched in 1953, 1954 and 1968 but no plants were found (Whitehead, 1976).

During the war, large areas around and including the site were cultivated and all remain under

cultivation or as improved grassland. There has also been planting of conifers in what were

presumably the less well-stocked parts of the woodland (Archibald, unpublished).

There is some controversy regarding the origins of the Llanrothal population. Perring and

Walters (1962) classify the Llanrothal population as indigenous after Hyde (1936). However,

both S. Thomson (BSBI recorder for Hereford, personal communication) and J.F. Archibald

(unpublished) strongly suspect that it was an introduction, perhaps thrown out of a garden. In

the absence of both plant and original habitat it is now impossible to be more conclusive.

2.2.5 *Summary of the historical records*

The historical evidence indicates that *L. urens* has tended to flourish in wet grassy heath and

grassland communities within clearings in or adjacent to present or former wooded sites. The

most striking and common feature of the various historical accounts is the revival of the species

following site disturbance. While many extinctions are a direct consequence of land use change

and the taking of former woodland and pasture into agriculture, given its common occurrence in

woodland, it is likely that *L. urens* prospered when coppicing was much more widely practised

and there was significant disturbance to the ground flora and a change to the light climate at

regular intervals (Rackham, 1986; Peterken, 1993). Decline in coppicing has thus resulted in

the gradual extinction of *L. urens* on many sites. Similarly, in grazed pasture, the species survives best where there has been trampling and disturbance by animals.

2.3 Survey of present-day floristic composition and environmental controls of plant communities containing *L. urens*

The conservation of *L. urens* requires an appraisal of the range of plant communities in which it grows and the environmental factors that determine the distribution of those communities. Thus a full survey of all six extant *L. urens* sites in southern England was completed in 1993.

2.3.1 *Sampling*

At each of the survey sites, a stratified sampling technique was used to ensure that the full ecological variation present was described (Kent & Coker, 1992). On a brief reconnaissance, a map of the site was sketched (e.g. Figure 2.3). This was then divided up into major community types on the basis of the vegetation structure and dominant species. The areas of *L. urens* were identified and marked on the site map (e.g. Figure 2.3).

Two quadrats were then allocated to each community type that contained *L. urens* as defined on the site map, one within the *L. urens* patch and a second outside, for comparison. Each community type that did not contain *L. urens* was allocated a single quadrat. Quadrats were placed in representative areas within the communities and sampling was thus deliberately biased in order to describe the maximum observed variation. The number of quadrats recorded per site were as follows: Redlake, 13; Andrew's Wood, 40; Kilmington, 4; Hurst Heath, 14; Hinton Admiral, 8; Flimwell, 16.

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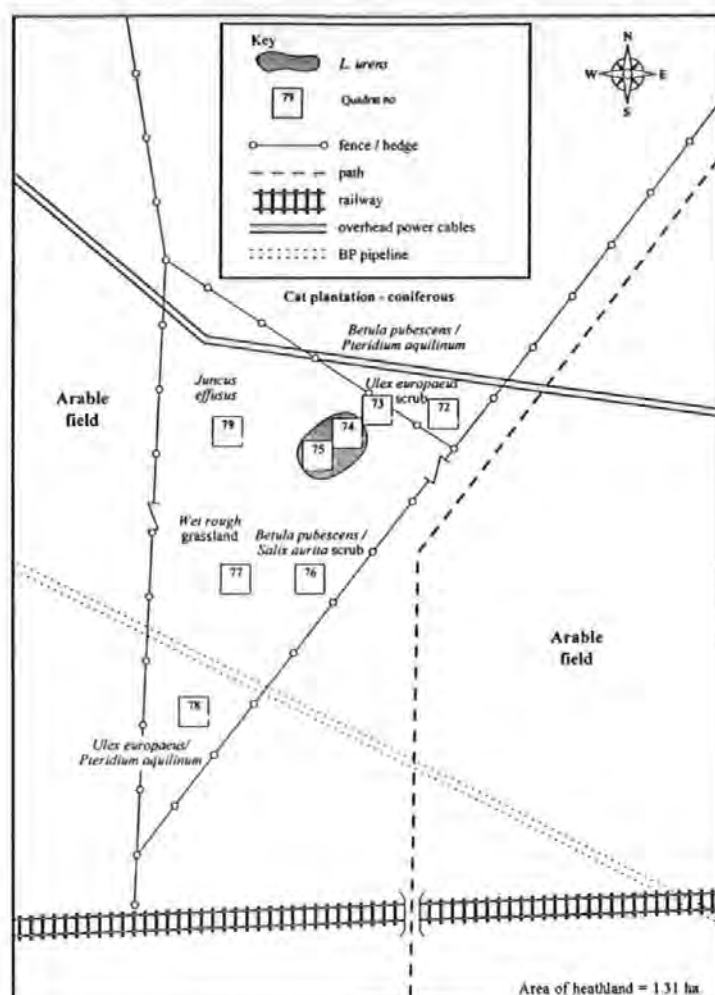
Figure 2.3: Sketch map of site of extant *L. urens* population near Hinton Admiral, Hampshire.

2.3.2 Collection of floristic data for phytosociology

Data were collected on the floristic composition in order to define the range of community types within which *L. urens* occurs in southern England.

The percentage cover of each species of higher plant present within a 0.5 x 0.5 m quadrat was recorded using an 11-point Domin scale. This subjective assessment of species abundance was chosen for speed and relative accuracy of measurement (Causton, 1988; Kent & Coker, 1992).

2.3.3 *Environmental data*

Environmental data were collected at each quadrat in order to determine the principal factors controlling the distribution and abundance of *L. urens* within those communities where it occurred. Data were gathered on interval, ordinal and nominal scales. Although nominal and ordinal data are weak in explaining variability when compared to interval data, they are still useful in characterising controlling environmental factors and in particular those variables measuring biotic pressure (Kent & Coker, 1992).

The following variables were recorded and a standard data record form (Figure 2.4) was completed for each quadrat. The survey was carried out during July 1993.

SITE RECORD FORM

Site	Grid Ref.
Date	Owner
Area	Altitude
Present use/conservation status	
Adjacent land	Situation
broadleaf wood	mixed wood	valley side	hill slope
conifer wood	scrub	valley bottom	hill top
lowland grass	parkland	plain	coastal
lowland heath	orchard	plateau	inland
upland grass	arable/ley		
upland heath	garden		
bog/peatland	fen		
moving water	still water		
buildings	road/railway		
Lobelia urens	Management history
Estimation of pop⁰ size	Time since last grazed
Degree of clumping:	Past grazing intensity
Size index Spacing index	Present grazing intensity
Notes:	Grazing vert. spp.
	Time since last soil disturbance
	Past disturbance intensity
	Past disturbance type
	Present disturbance intensity
	Present disturbance type
	Artificial enrichment

Figure 2.4: (a) Site recording sheet for floristic and environmental survey of *L. urens* sites.

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QUADRAT RECORD FORM

1. ENVIRONMENTAL DATA

Quadrat No.	Weather	Aspect
Slope	Drainage	Exposure
Sward height	RJFR	Microtopography
Litter abundance	Type of litter	Bryophyte cover
Bare ground	Invertebrates	Vertebrates

Disturbance/Management notes

Soil things:

Classification

Texture

Structure

Notes:

Lobelia urens

Lobelia absent		......distance to nearest plant
Lobelia present		......Abundance index

No. rosettes	No. branches	Ht. of spike	Notes

2. VASCULAR PLANT SPECIES

Quadrat No.	Abundance index									

Figure 2.4 (cont.): (b) Quadrat recording sheets for floristic and environmental survey of _L. urens_ sites.

Microclimate and habitat

(1) Ratio of red to far-red light Light which passes through the leaves of photosynthesizing plants exhibits a strong peak in the far-red region, centred on 730 nm (Smith, 1982), due to the chlorophyll absorption in the red region of the spectrum. As the total radiation decreases with sward/canopy thickness, the relative amount of far-red increases (Goodfellow & Barkham, 1974). Thus the ratio of red to far-red gives an index of the degree of canopy shade. This was measured using a Sky SKR 100 light meter.

(2) Height of the dominant vegetation Recording the height of the vegetation using a metre rule gave an indirect measurement of the degree of shade.

(3) Aspect Aspect affects the amount of sunlight received; Grace (1987) reports that there is an average temperature difference of 3°C between a north and a south facing slope and that this is equivalent to a latitudinal shift of 100 km. The aspect of sloping quadrats was recorded on an 8-point nominal scale representing compass bearings.

(4) Slope Slope affects drainage and is also connected with aspect, both of which directly affect temperature. A clinometer was used to measure the slope to the nearest degree.

(5-9) Bare ground, bryophyte cover, litter abundance, litter type and microtopography These five variables were chosen as measures of small-scale variations in the environment which may limit the availability of 'safe-sites' for the germination and establishment of seedlings. *Bare ground* can be used as a simple measure of sward density, since it was taken to be the proportion not covered by higher plants and did not include litter or bryophyte cover. *Bryophytes* alter the light and moisture availability of seedlings. *Plant litter* also affects light along with soil structure and is known to restrict germination in some species (Goldberg & Werner, 1983), as is microtopography (Harper *et al.*, 1965). The percentage cover of bare ground, bryophytes and litter was recorded on a Domin scale partitioned into six cover classes

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as follows: + less than 1%; 1 1-4%; 2 5-24%; 3 25-49%; 4 50-74%; 5 75-100%. The dominant species of the litter were also recorded. *Microtopography* was recorded on a 1 to 5 ordinal scale ranging from: 1, flat; through 3, uneven; to 5, deeply rutted/poached.

(10) Exposure The hypothesis that *L. urens* thrives in small woodland clearings was investigated in terms of exposure to the weather. A 5-point ordinal scale was used ranging from: 1, open; to 5, sheltered.

Soil variables

A screw auger was used to remove a soil core down to 40 cm and horizon depths were measured to the nearest cm.

(11) Soil texture Soil texture refers to the size distribution of the particles that make up the soil. 'Hand-texturing', using the tactile characteristics of the three main particle sizes, sand, silt and clay, was used as a measure soil texture. Following Courtney & Trudgill (1984), soils were categorised on a 6-point scale: sand, loamy sand, sandy loam, silty loam, clay loam, clay.

(12) Soil structure Increased compaction of soils is negatively correlated to root penetration, water availability and aeration. The degree of structural development was noted using the following scale:

Structureless: No observable peds; massive if coherent and single-grained if non-coherent

Weak: Indistinct peds; when disturbed the soil breaks into much aggregated material

Moderate: Well formed peds; little unaggregated soil when disturbed

Strong: Peds distinct in place; soil remains aggregated when disturbed

Soil bulk density Bulk density is defined as the ratio of mass to bulk or macroscopic volume of soil particles plus pore spaces in a sample (Rowell, 1994). In this study, bulk density was employed to convert the proportion by weight of nutrients, organic matter and soil moisture to

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content by volume. Since first, a number of widely differing soils were being compared, and second, plants exploit a volume of soil, not a weight. Five samples per site were positioned in order to describe within-site variability. A bulb planter was used to remove a core of earth approximately 10 cm long and 7 cm in diameter. The exact volume of the excavation was determined by filling the hole with sand, of which the volume per unit mass was known. The earth removed was air-dried and weighed and the mass expressed per unit volume (gcm^{-3}).

(13-22) Soil nutrient analyses The top 10 cm of cores extracted for the soil description were retained and air-dried for chemical analysis. The available ions were measured using acetic acid solution, a weak liberator of cations at exchange sites, since this extractant allows both the cations and phosphorus to be determined in the one extract (Allen, 1989).

Five grams of air-dried soil, milled to pass a 2 mm sieve were shaken with 50 ml of 5% glacial acetic in a 250 ml conical flask for 15 minutes. The solution was allowed to settle then filtered through a fluted Whatman qualitative no. 540 into a 100 ml volumetric flask. Further aliquots of acetic were added to the soil, swirled and allowed to settle, before filtering into the volumetric flask. The filtrate was then made up to 100 ml.

Several of the more important macro-nutrients were chosen to represent the underlying soil status: calcium, potassium, sodium, magnesium, and phosphorus. Data on nitrogen were not collected, due to the modifying effects of collection, transportation and storage (Allen, 1989). Calcium, potassium, sodium and magnesium were all analyzed by flame atomic absorption using a Varian 975 series atomic absorption spectrophotometer with auto-sampler. All samples were diluted 100 fold to reduce concentrations to within the scale of the spectrophotometer. Colorimetry was used to estimate the amount of dissolved reactive phosphorus in the soil extract. The method used follows the manual molybdenum blue method using stannous chloride reduction (Allen, 1989) and is particularly sensitive (Allen, 1989; Olsen & Sommers, 1982).

Since significant differences in soil bulk density were found between sites, the results were expressed both gravimetrically (mg per g of the element in air dried soil) and volumetrically (mg per cm^3 in air dried soil), using bulk density values for conversion.

(23) Soil pH Soil pH was measured on the same air dry sample from which the extracts had originally been taken. The method used a soil:water ratio of approximately 1:1 by volume, 5 g of soil to 12.5 ml of deionised water. Samples were placed on an automated shaker for 15 minutes, then allowed to stand for a further 15 minutes. The pH was then determined using a Russell 640 digital pH meter with automatic temperature correction.

(24-25) Organic matter content of soil Evaluation of the organic matter content of the soil was measured by loss on ignition following the method of Ball (1964). The weight loss following combustion of the soil sample was taken as an indication of organic matter content and was expressed both gravimetrically and volumetrically, using bulk density values for conversion.

(26) Drainage Drainage is an measure of the water retentive capacity of the soil. A 5-point scale was used to describe the drainage conditions at the sites sampled: 1 Very free; 2 Free; 3 Imperfect; 4 Poor; 5 Standing water.

(27-28) Soil moisture content Soil samples were collected from the surface horizon of all sites after heavy rain followed by a 48 hour drainage period (Cassel & Nielsen, 1986) on October 20 and 21 1993. Moisture was determined by oven drying and results were expressed both gravimetrically as gram of water per gram of fresh soil and volumetrically (gcm^{-3}), using the bulk density data for the conversion.

2.4 Data analysis

A total of 95 quadrats were collected from the six *L. urens* sites. These contained 122 species of higher plant including *L. urens* (Table 2.2).

Achillea millefolium	Eupatorium cannabinum	Prunella vulgaris
Achillea ptarmica	Fragaria vesca	Pteridium aquilinum
Agrostis canina	Festuca rubra	Pulicaria dysenterica
Agrostis capillaris	Filipendula ulmaria	Quercus robur
Agrostis curtisii	Galium palustre	Ranunculus acris
Agrostis stolonifera	Genista anglica	Ranunculus ficaria
Ajuga reptans	Geranium robertianum	Ranunculus flammula
Anagallis tenella	Hedera helix	Ranunculus repens
Angelica sylvestris	Hieracium pilosella	Raphanus raphanistrum
Anthoxanthum odoratum	Holcus lanatus	Rhododendron ponticum
Athyrium filix-femina	Hydrocotyle vulgaris	Rosa canina
Betula pubescens	Hypericum androsaemum	Rubus fruticosus agg.
Blechnum spicant	Hypericum humifusum	Rumex acetosa
Callitriche stagnalis	Hypericum pulchrum	Rumex acetosella
Calluna vulgaris	Hypericum tetrapterum	Salix aurita
Carduus crispus	Hypericum undulatum	Salix cinerea
Carex binervis	Hypochoeris glabra	Salix repens
Carex echinata	Hypochoeris radicata	Scirpus sylvaticus
Carex flacca	Juncus acutiflorus	Scutellaria minor
Carex hostiana	Juncus articulatus	Senecio jacobaea
Castanea sativa	Juncus bufonius	Senecio vulgaris
Centaurea nigra	Juncus conglomeratus	Serratula tinctoria
Centaurium erythraea	Juncus effusus	Solanum dulcamara
Chamerion angustifolium	Lamium purpureum	Stachys officinalis
Circaea lutetiana	Leontodon hispidus	Stellaria alsine
Cirsium dissectum	Leucanthemum vulgare	Stellaria graminea
Cirsium palustre	Lotus corniculatus	Succisa pratensis
Crepis biennis	Lotus uliginosus	Taraxacum officinale agg.
Cynosurus cristatus	Lonicera periclymenum	Teucrium scorodonia
Dactylorhiza maculata	Luzula campestris	Trifolium repens
Dactylorhiza praetermissa	Luzula multiflora	Ulex europaeus
Dactylis glomerata	Lychnis flos-cuculi	Ulex minor
Danthonia decumbens	Lysimachia nemorum	Urtica dioica
Deschampsia flexuosa	Mentha aquatica	Veronica chamaedrys
Digitalis purpurea	Molinia caerulea	Veronica montana
Dryopteris dilatata	Plantago lanceolata	Veronica scutellata
Dryopteris filix-mas	Plantago major	Viburnum opulus
Epilobium hirsutum	Poa trivialis	Viola lactea
Epilobium montanum	Polygonum hydropiper	Viola palustris
Erica cinerea	Potentilla erecta	Viola riviniana
Erica tetralix		

Table 2.2: Associates of *L. urens* in southern England.

Community classification and phytosociology

Classification of floristic data is based on the idea that community types exist and that these can be identified by characteristic species combinations. The aims of classification are to give information on the concurrence of species, to establish community types for descriptive studies (phytosociology) and to detect relations between these community types and the environment by external analysis (van Tongeren, 1987). In order to define and examine the variability of the plant communities in which *L. urens* occurs, the floristic data were classified using Two-Way Indicator Species Analysis and the computer program TWINSPAN (Hill, 1979a). The TABLEFIT program (Hill, 1993) was then used to link the resulting communities to the categories of the National Vegetation Classification (NVC) (Rodwell, 1991a; b).

Examination of environmental gradients (ordination) and correlations with community and species distributions

In contrast to classification, the emphasis of ordination lies on individual quadrats or species and the variation between them. The data are ordered along a gradient which shows the maximum variation among them. The ordering is continuous rather than discrete. The gradient(s) produced are correlated, either directly or indirectly, to underlying environmental factors. Indirect ordination methods (Hill, 1973; 1979b; Hill & Gauch, 1980) distribute floristic data along two or more axes which represent the gradients of maximum variation in the data set. Most interpretation is carried out by superimposing environmental data onto the axes of the quadrat ordination diagram. Multivariate direct gradient analysis was developed recently as an extension of the indirect gradient analysis (Jongman *et al.*, 1987; ter Braak, 1987). It is a constrained ordination technique since the floristic ordination axes are restricted to be linear combinations of the environmental variables. The amount of variation within the data that is accounted for by each axis is described by an eigenvalue, on a scale of 0-1.

The statistical validity of the resulting environmental axes and the ordination as a whole can be evaluated by an unrestricted Monte Carlo permutations test (ter Braak, 1987). The test is

carried out by randomly permutating the sample numbers in the environmental data and then recalculating the first eigenvalue and the sum of all eigenvalues (trace). If the species abundances are significantly related to the examined environmental variables then the values calculated from the original data are among the highest 5% of the values calculated from at least 100 random data sets. The first eigenvalue is used for testing the importance of the first ordination axis. The trace is used for an overall test of the effect of the environmental variables on the species.

Canonical Correspondence Analysis (CCA), using the CANOCO computer program (ter Braak, 1986; 1987; 1992; Jongman *et al.*, 1987) was applied to the floristic and environmental data, with Principal Component Analysis (PCA) being used to examine redundancy and intercorrelation among the environmental variables.

Data were analysed through TWINSPAN and CCA programs in two formats:
(i) regional analyses, on the full data set across all six sites;
(ii) local analyses, for each site individually.

2.5 Results

2.5.1 *Regional analyses*

Variability of environmental factors between sites

Table 2.3 presents summary data for the environmental factors from the six sites individually and across all sites. Some factors show comparatively little variation between the sites. For example, the average pH across all sites is at 4.86, with the means of the six sites ranging from 4.25 to 5.06. Similarly, most of the soil chemistry variables are relatively uniform. The overall picture is of a species growing on seasonally wet, moderately acid and nutrient-poor soils, within sheltered low-sloping sites distributed across a range of aspects. In contrast, other measured environmental factors show greater differences. *L. urens* grows within a full range of

			Site.					
Environmental Variable.		Redlake, Cornwall.	Andrew's Wood, Devon.	Kilmington, Devon.	Hurst Heath, Dorset.	Hinton Admiral, Hampshire.	Flimwell, Sussex.	All sites.
1	R:FR (see text)							
	Mean	0.382	0.695	0.403	0.635	0.551	0.700	0.620
	Max	0.650	1.100	0.620	1.130	1.080	1.000	1.130
	Min	0.100	0.080	0.250	0.070	0.200	0.150	0.070
	S.D.	0.184	0.270	0.176	0.396	0.323	0.288	0.304
2 *	Vegetation height (cm):							
	Mean	62.460	30.720	35.250	38.930	70.200	45.000	47.200
	Max	111.000	186.000	45.000	74.000	137.000	120.000	186.000
	Min	40.000	0.000	28.000	6.000	31.000	1.000	0.000
	S.D.	1.660	35.520	8.180	22.780	36.500	33.980	33.540
3	Aspect (see text):							
	Mean	4.538	5.200	7.000	9.000	6.000	5.625	5.884
	Max	2.000	6.000	7.000	9.000	6.000	9.000	9.000
	Min	6.000	5.000	7.000	9.000	6.000	3.000	0.000
	S.D.	3.307	0.405	0.000	0.000	0.000	1.360	1.929
4 *	Slope (see text):							
	Mean	2.308	4.575	8.000	0.000	1.000	2.437	3.053
	Max	10.000	8.000	8.000	0.000	1.000	5.000	10.000
	Min	0.000	2.000	8.000	0.000	1.000	0.000	0.000
	S.D.	3.093	1.797	0.000	0.000	0.000	1.313	2.586
5	Bare ground (see text):							
	Mean	1.077	3.250	1.000	2.786	1.500	2.937	2.589
	Max	2.000	6.000	1.000	5.000	4.000	6.000	6.000
	Min	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	S.D.	0.277	1.515	0.000	1.528	1.069	1.652	1.595
6	Bryophyte cover (see text):							
	Mean	1.615	1.675	1.000	1.857	1.750	1.937	1.716
	Max	6.000	6.000	1.000	5.000	3.000	5.000	6.000
	Min	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	S.D.	1.557	1.095	1.000	1.406	1.035	1.389	1.226
7 *	Litter abundance (see text):							
	Mean	3.846	3.000	4.750	3.429	4.375	2.062	3.211
	Max	6.000	6.000	5.000	6.000	6.0000	6.000	6.000
	Min	2.000	1.000	4.000	1.000	2.000	1.000	1.000
	S.D.	1.345	1.895	0.500	1.828	1.188	1.289	1.756
8	Litter type (see text).							
	Mean	1.769	2.425	1.000	1.000	2.250	4.000	2.316
	Max	4.000	7.000	1.000	3.000	7.000	8.000	8.000
	Min	1.000	0.000	1.000	0.000	1.000	0.000	0.000
	S.D.	0.927	2.037	0.000	0.679	2.185	3.596	2.275
9 *	Micro-topography (see text)							
	Mean	2.692	2.850	1.000	2.071	1.875	3.125	2.600
	Max	4.000	5.000	1.000	5.000	5.000	5.000	5.000
	Min	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	S.D.	1.032	1.027	0.000	1.269	1.458	1.088	1.189
10 *	Exposure (see text)							
	Mean	4.846	4.425	4.000	5.000	3.625	4.125	4.432
	Max	5.000	5.000	4.000	5.000	4.000	5.000	5.000
	Min	4.000	4.000	4.000	5.000	3.000	3.000	3.000
	S.D.	0.376	0.501	0.000	0.000	0.518	0.619	0.595
11 *	Soil texture (see text):							
	Mean	4.000	4.000	4.000	3.214	3.000	5.625	4.074
	Max	4.000	4.000	4.000	4.000	3.000	6.000	6.000
	Min	4.000	4.000	4.000	3.000	3.000	4.000	3.000
	S.D.	0.000	0.000	0.000	0.426	0.000	0.619	0.841
12 *	Soil structure (see text)							
	Mean	2.154	2.050	3.000	3.000	2.000	2.125	2.253
	Max	3.000	3.000	3.000	4.000	2.000	3.000	4.000
	Min	1.000	2.000	3.000	2.000	2.000	2.000	1.000
	S.D.	0.555	0.221	0.000	0.392	0.000	0.347	0.483
13	Calcium (mg/g)							
	Mean	1.378	2.175	1.630	2.450	1.488	1.385	1.893
	Max	2.840	11.240	2.340	4.340	1.740	2.660	11.240
	Min	0.280	0.280	1.080	1.300	1.240	0.840	0.280
	S.D.	0.932	2.307	0.537	0.936	0.168	0.579	1.638
14	Potassium (mg/g)							
	Mean	0.256	0.188	0.248	0.326	0.397	0.113	0.225
	Max	1.160	0.520	0.440	0.900	0.805	0.400	1.160
	Min	0.0328	0.029	0.051	0.026	0.037	0.020	0.020
	S.D.	0.338	0.149	0.161	0.270	0.287	0.140	0.225

Table 2.3: Means, standard deviations, maxima and minima of the 28 variables measured in the survey of *L. urens* at the six sites in southern England. Asterisk denotes variables used in final analyses (see p. 67).

Environmental Variable		Redlake, Cornwall.	Andrew's Wood, Devon.	Kilmington, Devon.	Hurst Heath, Dorset.	Hinton Admiral, Hampshire.	Flimwell, Sussex.	All sites.
15 Sodium (mg/g):	Mean	0.049	0.041	0.054	0.037	0.032	0.025	0.039
	Max	0.075	0.079	0.071	0.067	0.058	0.060	0.079
	Min	0.028	0.005	0.033	0.020	0.018	0.015	0.005
	S.D.	0.014	0.014	0.016	0.013	0.012	0.011	0.015
16 Magnesium (mg/g):	Mean	0.194	0.243	0.241	0.196	0.082	0.061	0.185
	Max	0.537	0.639	0.288	0.484	0.107	0.130	0.639
	Min	0.076	0.048	0.159	0.060	0.053	0.027	0.027
	S.D.	0.136	0.122	0.057	0.124	0.019	0.030	0.127
17 Phosphorus (mg/g):	Mean	0.008	0.002	0.002	0.002	0.002	0.004	0.003
	Max	0.024	0.008	0.003	0.008	0.005	0.007	0.024
	Min	0.001	0.000	0.001	0.000	0.000	0.001	0.000
	S.D.	0.007	0.002	0.001	0.002	0.002	0.002	0.004
18 * Calcium (mg/cm³)	Mean	0.679	1.986	0.994	1.519	1.443	1.806	1.620
	Max	1.505	9.666	1.427	2.691	1.688	3.431	9.666
	Min	0.04	0.241	0.659	0.806	1.203	1.084	0.040
	S.D.	0.484	2.310	0.327	0.580	0.163	0.743	1.609
19 * Potassium (mg/cm³):	Mean	0.136	0.152	0.148	0.246	0.425	0.146	0.185
	Max	0.615	0.447	0.268	0.868	0.781	0.516	0.868
	Min	0.017	0.035	0.031	0.016	0.050	0.025	0.016
	S.D.	0.179	0.126	0.099	0.245	0.242	0.180	0.188
20 * Sodium (mg/cm³):	Mean	0.026	0.035	0.033	0.023	0.031	0.033	0.032
	Max	0.040	0.068	0.044	0.042	0.056	0.078	0.078
	Min	0.015	0.004	0.020	0.013	0.017	0.020	0.004
	S.D.	0.007	0.012	0.010	0.008	0.011	0.014	0.012
21 * Magnesium (mg/cm³)	Mean	0.103	0.208	0.147	0.122	0.080	0.079	0.146
	Max	0.284	0.549	0.175	0.300	0.104	0.168	0.549
	Min	0.040	0.041	0.097	0.037	0.051	0.035	0.035
	S.D.	0.072	0.104	0.035	0.077	0.018	0.039	0.097
22 * Phosphorus (mg/cm³):	Mean	0.004	0.002	0.002	0.001	0.002	0.006	0.002
	Max	0.013	0.007	0.003	0.007	0.005	0.009	0.013
	Min	0.001	0.000	0.001	0.000	0.000	0.001	0.000
	S.D	0.004	0.001	0.001	0.002	0.002	0.002	0.003
23 * Soil pH (see text)	Mean	5.056	5.059	4.607	4.744	4.254	4.696	4.864
	Max	6.060	5.910	4.940	5.810	4.430	5.150	6.150
	Min	4.470	3.900	4.230	3.680	4.040	3.700	3.680
	S.D.	0.472	0.491	0.346	0.609	0.156	0.703	0.572
24 Organic matter content (g/g)	Mean	17.610	16.680	6.612	16.960	11.889	8.830	14.700
	Max	30.800	35.370	6.830	30.060	16.000	33.400	35.370
	Min	8.940	5.240	6.390	5.750	9.820	2.970	2.970
	S.D.	6.620	7.020	0.181	8.060	2.090	7.720	7.601
25 * Organic matter content (g/cm³)	Mean	9.335	14.284	4.035	10.510	7.360	5.480	10.554
	Max	16.320	30.420	4.170	18.640	9.920	20.710	30.420
	Min	4.740	4.020	3.900	3.570	6.010	1.840	1.840
	S.D.	3.506	6.131	0.110	5.000	1.309	4.780	6.131
26 Drainage (see text)	Mean	2.769	2.725	2.000	2.143	2.625	3.062	2.663
	Max	5.000	5.000	2.000	3.000	4.000	4.000	5.000
	Min	1.000	2.000	2.000	2.000	2.000	2.000	1.000
	S.D	1.235	0.933	0.000	0.363	0.916	0.443	0.870
27 Moisture content (g/g)	Mean	43.020	39.770	17.450	30.810	26.570	24.970	34.350
	Max	53.300	55.800	20.200	38.200	38.600	50.100	55.800
	Min	23.300	28.900	15.300	24.400	17.800	16.300	15.300
	S.D.	9.430	7.370	2.150	4.650	6.500	9.050	10.500
28 * Moisture content (g/cm³)	Mean	22.600	34.330	10.625	19.043	27.100	31.110	28.312
	Max	28.200	48.000	12.300	23.700	37.400	64.600	64.600
	Min	12.300	24.800	9.300	15.100	17.300	21.100	9.300
	S.D.	5.000	6.340	1.320	2.914	5.880	11.320	9.556

Table 2.3 (continued): Means, standard deviations, maxima and minima of the 28 variables measured in the survey of *L. urens* at the six sites in southern England. Asterisk denotes variables used in final analyses (see p. 67).

soil texture and structures in the surface horizons. Organic matter content is also highly variable across sites. *L. urens* show no relationship with the cover of bryophytes or plant litter, proportion of bare ground, microtopography, aspect or sward height.

Interpretation of two-way indicator species analysis and definition of plant communities at the regional scale

The classification groups resulting from the TWINSPAN analysis are shown in Table 2.4. Six quadrat groups were defined (A-F).

Groups A and B were the rough grassland communities of Redlake, Cornwall and Andrew's Wood, Devon. The TABLEFIT program indicated that these were typical of M25c - *Molinia caerulea-Potentilla erecta* mire containing *L. urens* with varying associated species (Table 2.5). In Group A, *Molinia caerulea, Rubus fruticosus, Holcus lanatus, Lotus uliginosus, Potentilla erecta, Mentha aquatica, Pulicaria dysenterica* and *Plantago lanceolata* were common. In Group B, *Molinia caerulea* and *Potentilla erecta* were again the key indicators, but the main associated species were *Cirsium palustre, Juncus conglomeratus* and *Angelica sylvestris. Betula pubescens* was an important shrub species.

Group C was a small group of quadrats at Andrew's Wood, Devon in which *Molinia caerulea* and *Potentilla erecta* were poorly represented and where *Rubus fruticosus* and *Hedera helix* dominated. This indicated woodland communities from which *L. urens* was excluded except in more open areas, corresponding to NVC types W23 and W24 (Table 2.5). Again, *Betula pubescens* occurred in a number of quadrats.

The eastern quadrats from Kilmington, Devon; Hurst Heath, Dorset; Hinton Admiral, Hampshire and Flimwell, Sussex were split between groups D and E (Table 2.4). Group D was a large and relatively uniform group dominated by *Molinia caerulea* and *Potentilla erecta* with *L. urens* occurring as a preferential species. A large number of associated species occurred with few of the common members of the western sites at Redlake, Cornwall and Andrew's Wood in Devon.

Species	A	B	C	D	E	F	Species
63. Juncus articulatus	III 5	II 4	III 3				Juncus articulatus
81. Poa trivialis	I 3		II 3				Poa trivialis
86. Pulicaria dysenterica	IV 3	III 3	II 3				Pulicaria dysenterica
90. Ranunculus flammula	II 2	+ 3					Ranunculus flammula
108. Stellaria alsine	I 3	+ 3	II 3				Stellaria alsine
8. Anagallis tenella	I 3	+ 5					Anagallis tenella
77. Mentha aquatica	III 3	III 3	III 3				Mentha aquatica
28. Circaea lutetiana		+ 2					Circaea lutetiana
36. Deschampsia flexuosa	I 3	III 3					Deschampsia flexuosa
38. Dryopteris dilatata		+ 3					Dryopteris dilatata
55. Hypericum androsaemum		+ 3					Hypericum androsaemum
65. Juncus conglomeratus	I 5	IV 3	III 3	+ 3			Juncus conglomeratus
75. Lychnis flos-cuculi		+ 2					Lychnis flos-cuculi
82. Polygonum hydropiper		+ 2					Polygonum hydropiper
110. Succisa pratensis	I 4	II 3					Succisa pratensis
7. Ajuga reptans		+ 3	II 2				Ajuga reptans
11. Athyrium filix-femina			II 2				Athyrium filix-femina
15. Callitriche stagnalis		+ 5					Callitriche stagnalis
19. Carex echinata		I 3					Carex echinata
21. Carex hostiana		+ 5					Carex hostiana
39. Dryopteris filix-mas		+ 3	II 4				Dryopteris filix-mas
40. Epilobium hirsutum			II 2				Epilobium hirsutum
45. Fragaria vesca		+ 2	II 5				Fragaria vesca
58. Hypericum tetrapterum			II 3				Hypericum tetrapterum
64. Juncus bufonius		III 3	II 3				Juncus bufonius
68. Leontodon hispidus		+ 2					Leontodon hispidus
70. Lotus corniculatus		II 3					Lotus corniculatus
120. Viburnum opulus	I 2		II 4				Viburnum opulus
122. Viola palustris	I 2	III 2	IV 2		I 3		Viola palustris
9. Angelica sylvestris	II 3	IV 3	IV 3	+ 3			Angelica sylvestris
30. Cirsium palustre	III 3	V 3	III 3	I 3	I 3		Cirsium palustre
48. Galium palustre	I 3	III 3	IV 3	I 3	I 4		Galium palustre
99. Salix cinerea	I 3	II 3	II 4		I 3		Salix cinerea
46. Festuca rubra	I 4	III 4		I 3			Festuca rubra
62. Juncus acutiflorus	I 3	III 5		I 3			Juncus acutiflorus
50. Geranium robertianum	I 3		II 2				Geranium robertianum
2. Achillea ptarmica	I 2						Achillea ptarmica
6. Agrostis stolonifera	I 4						Agrostis stolonifera
17. Carduus crispus	I 3						Carduus crispus
33. Dactylorhiza maculata	I 3						Dactylorhiza maculata
34. Dactylorhiza praetermissa	I 3						Dactylorhiza praetermissa
35. Dactylis glomerata	II 3						Dactylis glomerata
47. Filipendula ulmaria	I 4						Filipendula ulmaria
54. Hydrocotyle vulgaris	II 3	+ 4					Hydrocotyle vulgaris
73. Luzula campestris	I 3						Luzula campestris
88. Ranunculus acris	I 3						Ranunculus acris
89. Ranunculus ficaria	I 3						Ranunculus ficaria
119. Veronica scutellata	I 2						Veronica scutellata
24. Centaurea nigra	IV 3	+ 2		I 4			Centaurea nigra
53. Holcus lanatus	IV 3	III 3		II 4			Holcus lanatus
71. Lotus uliginosus	V 3	III 4		I 3			Lotus uliginosus
79. Plantago lanceolata	IV 4	II 3		I 5			Plantago lanceolata
96. Rumex acetosa	I 3	+ 3		+ 3			Rumex acetosa
31. Hedera helix	I 2		III 3		I 5		Hedera helix
95. Rubus fruticosus	V 3	III 3	V 4	III 3	V 4		Rubus fruticosus
98. Salix aurita	I 3	III 4		+ 3	II 3		Salix aurita
118. Veronica montana			II 2		I 2		Veronica montana
72. Lonicera periclymenum			III 4	+ 3	III 4		Lonicera periclymenum
76. Lysimachia nemorum	I 3	+ 2	II 3	I 3	I 3		Lysimachia nemorum
85. Pteridium aquilinum		II 3	III 4	I 3	IV 4		Pteridium aquilinum
116. Urtica dioica			II 3	+ 3			Urtica dioica
41. Epilobium montanum		+ 3	II 2	I 3			Epilobium montanum
69. Lobelia urens	III 3	IV 3	II 5	IV 3	II 4		Lobelia urens
78. Molinia caerulea	V 4	VI 4		V 4	IV 4		Molinia caerulea
107. Solanum dulcamara			II 3	+ 4			Solanum dulcamara
57. Hypericum pulchrum		I 2		I 3	I 2		Hypericum pulchrum
80. Plantago major	II 3			II 3			Plantago major
83. Potentilla erecta	III 3	IV 3	II 3	V 4	II 3		Potentilla erecta
111. Taraxacum officinale agg.	II 3			I 3			Taraxacum officinale agg.
1. Achillea millefolium	I 4			I 3			Achillea millefolium
91. Ranunculus repens		+ 3	II 5	II 4	I 3		Ranunculus repens
109. Stellaria graminea	I 2			I 3			Stellaria graminea
12. Stachys officinalis					I 3		Stachys officinalis
23. Castanea sativa					III 4		Castanea sativa

Table 2.4 Species composition of the six community types defined by two-way indicator species analysis of the quadrat data from the six extant sites of *Lobelia urens* L. in southern England. The first column corresponds to species constancy within each TWINSPAN group (I = 5% or less; II = 6-20%; III = 21-40%; IV = 41-60%; V = 61-80%; VI= 81-100%). The second column indicates average species abundance for each group on the domin scale.

Species	A	B	C	D	E	F	Species
Twinspan group							
26. Chamerion angustifolium					II 4		Chamerion angustifolium
67. Lamium purpureum					I 3		Lamium purpureum
4. Agrostis capillaris				+ 3			Agrostis capillaris
3. Agrostis canina				+ 4			Agrostis canina
25. Centaurium erythraea				II 3			Centaurium erythraea
27. Leucanthemum vulgare				+ 3			Leucanthemum vulgare
32. Cynosurus cristatus				+ 2			Cynosurus cristatus
60. Hypochoeris glabra				I 3			Hypochoeris glabra
61. Hypochoeris radicata				I 4			Hypochoeris radicata
84. Prunella vulgaris				II 3	I 3		Prunella vulgaris
101. Scirpus sylvaticus				II 3			Scirpus sylvaticus
103. Senecio jacobaea				I 3			Senecio jacobaea
104. Senecio vulgaris				+ 3			Senecio vulgaris
105. Serratula tinctoria				II 4			Serratula tinctoria
113. Trifolium repens				I 3			Trifolium repens
14. Blechnum spicant				+ 3	I 2		Blechnum spicant
49. Genista anglica				+ 3	I 2		Genista anglica
93. Rhododendron ponticum				I 3	III 4		Rhododendron ponticum
66. Juncus effusus	I 3			III 4			Juncus effusus
94. Rosa canina				+ 3			Rosa canina
102. Scutellaria minor		I 3		II 3			Scutellaria minor
5. Agrostis curtisii				+ 4			Agrostis curtisii
18. Carex binervis				II 3			Carex binervis
20. Carex flacca				+ 3			Carex flacca
29. Cirsium dissectum				II 3	II 3		Cirsium dissectum
31. Crepis biennis				I 4	I 2		Crepis biennis
42. Erica cinerea				I 3	I 2		Erica cinerea
43. Erica tetralix		I 3		II 4			Erica tetralix
44. Eupatorium cannabinum				+ 5			Eupatorium cannabinum
52. Hieracium pilosella				I 3			Hieracium pilosella
59. Hypericum undulatum				+ 2			Hypericum undulatum
74. Luzula multiflora				+ 2			Luzula multiflora
92. Raphanus raphanistrum				I 4			Raphanus raphanistrum
97. Rumex acetosella				I 3			Rumex acetosella
100. Salix repens				+ 3			Salix repens
106. Danthonia decumbens				I 4			Danthonia decumbens
115. Ulex minor				I 3	I 3		Ulex minor
117. Veronica chamaedrys				I 2			Veronica chamaedrys
121. Viola lactea				I 3			Viola lactea
123. Viola riviniana				II 3	I 4		Viola riviniana
13. Betula pubescens	I 4	IV 3	IV 2	III 3	III 3	IV 3	Betula pubescens
16. Calluna vulgaris					I 5	IV 4	Calluna vulgaris
114. Ulex europaeus	I 3				II 3	IV 5	Ulex europaeus
37. Digitalis purpurea				+ 3		IV 4	Digitalis purpurea
56. Hypericum humifusum				+ 2		IV 2	Hypericum humifusum
87. Quercus robur				+ 4		IV 4	Quercus robur
112.Teucrium scorodonia		+ 2		II 3	III 3	VI 3	Teucrium scorodonia
10. Anthoxanthum odoratum				III 3		IV 4	Anthoxanthum odoratum

Table 2.4 (continued): Species composition of the six community types defined by two-way indicator species analysis of the quadrat data from the six extant sites of *Lobelia urens* L. in southern England. The first column corresponds to species constancy within each TWINSPAN group (I = 5% or less; II = 6-20%; III = 21-40%; IV = 41-60%; V = 61-80%; VI= 81-100%). The second column indicates average species abundance for each group on the domin scale.

Two-way indicator species group	NVC Communities
A	M25 - *Molinia caerulea-Potentilla erecta* mire
B	M25c - *Molinia caerulea-Potentilla erecta* mire
C	W23 - *Ulex europaeus-Rubus fruticosus* scrub W25 - *Pteridium aquilinum-Rubus fruticosus* under scrub
D	M25 - *Molinia caerulea-Potentilla erecta* mire H3 - *Ulex minor-Agrositis curtisii* heath
E	W23 - *Ulex europaeus-Rubus fruticosus* scrub W25 - *Pteridium aquilinum-Rubus fruticosus* under scrub
F	W23 - *Ulex europaeus-Rubus fruticosus* scrub

Site	NVC Communities
Redlake, Cornwall.	M25 - *Molinia caerulea-Potentilla erecta* mire W23 - *Ulex europaeus-Rubus fruticosus* scrub
Andrew's Wood, Devon.	M25 - *Molinia caerulea-Potentilla erecta* mire W23 - *Ulex europaeus-Rubus fruticosus* scrub
Kilmington, Devon.	M25 - *Molinia caerulea-Potentilla erecta* mire W25 - *Pteridium aquilinum-Rubus fruticosus* under scrub
Hurst Heath, Dorset.	H3 - *Ulex minor-Agrositis curtisii* heath W25 - *Pteridium aquilinum-Rubus fruticosus* under scrub
Hinton Admiral, Hampshire.	H3 - *Ulex minor-Agrositis curtisii* heath W25 - *Pteridium aquilinum-Rubus fruticosus* under scrub
Flimwell, Sussex.	M25 - *Molinia caerulea-Potentilla erecta* mire W25 - *Pteridium aquilinum-Rubus fruticosus* under scrub

Table 2.5: NVC communities matched with the two-way indicator species analysis groups and the NVC communities present at each of the six survey sites.

This community was more heathy than typical M25, a mixture of NVC types M25 and H3/H4 (Table 2.5).

The 13 quadrats which made up group E were from woodland/scrub communities across all the sites. Characterised by *Lonicera periclymenum, Pteridium aquilinum, Rhododendron ponticum, Rubus fruticosus* and *Ulex europaeus*, they were classified as NVC W23 and W25, underscrub communities (Table 2.5). *L. urens* occurred in only two of the quadrats in this group and most quadrats thus represent samples taken adjacent to but not containing *L. urens* plants. This indicates the preference of *L. urens* for heathy clearings or gaps within woodland and

demonstrates that it does not grow in association with these more typical acidic woodland ground flora species.

The outlying group F was produced by the first TWINSPAN division, comprising quadrats 72 and 87 (Table 2.4). Both were dominated by scrub, with no *L. urens* present. Quadrat 72 was characterised by *Ulex europaeus, Calluna vulgaris* and *Quercus robur*, corresponding to NVC group H1 - *Calluna vulgaris-Festuca ovina* heath. In contrast, quadrat 87 contained *Digitalis purpurea, Anthoxanthum odoratum* and *Betula pubescens*, corresponding to NVC group W23c: *Ulex europaeus - Rubus fruticosus* scrub *Teucrium scorodonia* sub-community.

The phytosociological analyses show that *L. urens* is a species of heathy and acid grassland communities, typically dominated by *Molinia caerulea* within woodland and scrub. *L. urens* is not, however, a true ground flora species of acid woodland. This characteristic may explain its present situation as a threatened species, since with changes in woodland management, the open grass-heath areas within such wooded sites have become either overgrown in the absence of woodland management and coppicing, or have been drained and reclaimed for agriculture and grazing.

Interpretation of the regional direct ordination using canonical correspondence analysis
Initially, in order to examine relationships between floristic variation and environmental factors, the full floristic and environmental data sets (95 quadrats, 122 plant species and 28 environmental variables) were analysed by CCA. Figure 2.5 illustrates the first two axes of the resulting biplot of the quadrats combined with the environmental variables. The eigenvalues were 0.503 for the first axis and 0.445 for the second. The Monte Carlo permutations test (ter Braak, 1987; 1992) showed that these twenty-eight environmental variables explained a significant proportion of the variation present ($P<0.01$).
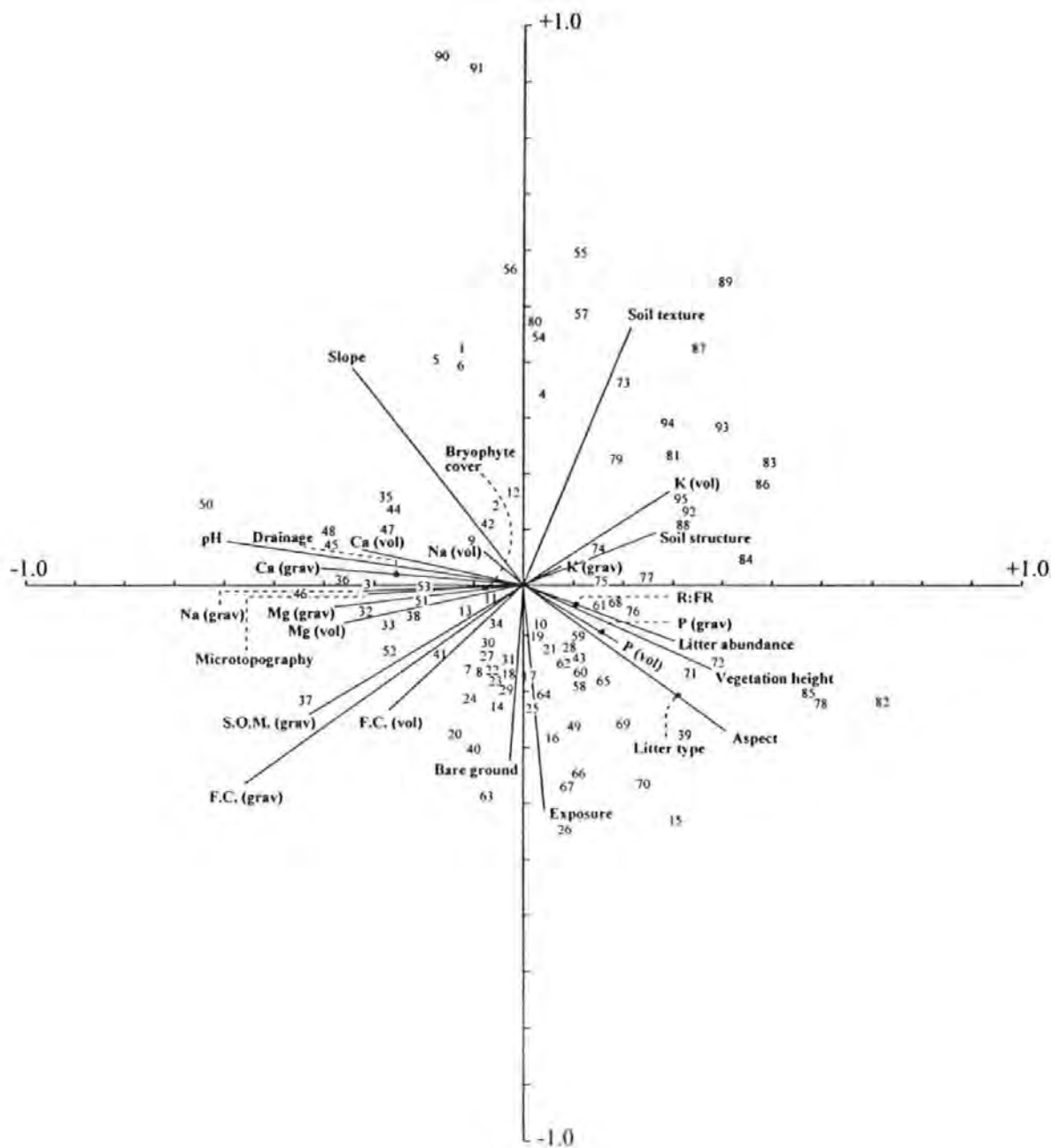
Figure 2.5: Quadrat-environmental biplot from canonical correspondence analysis of the 95 quadrats from the six sites, using all 28 environmental variables (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity; (grav) = results expressed gravimetrically; (vol) = results expressed volumetrically).

Removal of redundant environmental variables

The analysis also indicated, however, that a number of the environmental variables were contributing very little to the overall variance explained or were highly inter-correlated and thus redundant.

Using the quadrat/environmental biplot from CANOCO (Figure 2.5), the correlation matrix (Table 2.6) and the results of a Principal Component Analysis (PCA) of the 28 environmental variables (Figure 2.6), a number of variables were removed from the analysis.

a) Those shown to have a low explanatory power:

1. R:FR;

6. bryophyte cover.

b) Those variables measured on a nominal scale which contributed little explanation:

3. Aspect;

8. litter type.

c) Those shown to be highly correlated with another variable (in parentheses):

13. Calcium gravimetrically (volumetrically);

14. potassium gravimetrically (volumetrically);

15. sodium gravimetrically (volumetrically);

16. magnesium gravimetrically (volumetrically);

17. phosphorus gravimetrically (volumetrically);

25. organic matter content gravimetrically (volumetrically);

26. drainage (with soil moisture content);

27. moisture at field capacity gravimetrically (volumetrically).

	Slope	Drainage	Exposure	Vegetation height	r:fr	Microtopography	Litter abundance	Litter type	Bryophyte cover	Bare ground	Soil texture	Soil structure	pH	S.O.M. (grav)	F.C (grav)	P (grav)	Ca (grav)	Mg (grav)	Na (grav)	K (grav)	S.O.M (vol)	F.C (vol)	P (vol)	Ca (vol)	Mg (vol)	Na (vol)
Slope	-0.12																									
Drainage	-0.18	-0.04																								
Exposure	0.02	-0.45	0.09																							
Vegetation height	0.05	-0.23	0.13	0.02																						
r:fr	0.04	-0.05	-0.08	-0.06	-0.54																					
Microtopography	0.16	-0.03	0.56	0.00	-0.03	0.07																				
Litter abundance	-0.10	-0.05	-0.20	0.25	0.41	-0.36	-0.24																			
Litter type	-0.16	-0.00	-0.02	-0.06	0.18	0.13	-0.04	0.12																		
Bryophyte cover	0.01	-0.06	-0.17	0.09	-0.20	0.32	-0.14	-0.15	0.13																	
Bare ground	0.02	0.06	0.07	0.03	-0.19	0.45	0.19	-0.14	0.23	-0.04																
Soil texture	-0.28	0.17	0.27	-0.17	0.01	0.07	0.33	-0.20	0.33	-0.04	0.09															
Soil structure	0.49	-0.01	-0.53	0.09	-0.04	-0.03	-0.53	0.11	-0.19	0.07	-0.07	-0.27														
pH	-0.19	0.12	0.17	0.03	-0.19	0.17	0.21	-0.34	-0.22	-0.05	0.18	-0.09	-0.07													
S.O.M. (grav)	-0.07	-0.01	0.12	0.08	0.03	-0.13	0.10	0.01	-0.13	0.01	-0.05	-0.21	0.01	0.23												
F.C (grav)	-0.32	-0.04	0.46	0.18	0.06	-0.14	0.36	-0.09	-0.04	-0.03	0.01	-0.16	-0.41	0.38	0.59											
P (grav)	0.22	-0.05	-0.24	0.01	0.00	0.06	-0.22	-0.05	-0.18	-0.15	0.06	-0.32	0.31	0.07	-0.05	-0.15										
Ca (grav)	0.02	0.07	0.19	-0.13	-0.15	0.08	0.20	-0.30	-0.12	-0.04	0.16	-0.16	0.05	0.53	0.35	0.29	0.05									
Mg (grav)	-0.02	0.20	0.06	0.15	-0.18	0.05	-0.02	-0.12	-0.24	-0.09	0.15	-0.25	0.07	0.53	0.24	0.33	0.16	0.58								
Na (grav)	-0.18	0.22	0.21	0.07	0.21	-0.40	0.01	0.24	-0.22	-0.35	-0.01	-0.15	0.02	0.25	0.24	0.33	0.12	0.34	0.52							
K (grav)	0.08	-0.18	0.38	0.19	0.34	-0.20	0.19	0.09	0.03	-0.13	-0.18	0.16	0.30	0.17	0.01	0.20	-0.14	-0.21	-0.12	0.18						
S.O.M (vol)	-0.13	0.17	0.10	-0.05	-0.10	-0.01	0.13	-0.09	-0.11	0.00	0.09	-0.17	-0.06	0.32	0.92	0.58	-0.08	0.44	0.35	0.24	-0.14					
F.C (vol)	-0.33	0.11	0.45	-0.24	-0.06	0.07	0.39	-0.33	0.19	0.03	0.25	0.20	-0.50	0.22	0.30	0.66	-0.22	0.28	0.14	0.04	-0.03	0.48				
P (vol)	0.19	-0.12	-0.18	-0.07	0.02	0.10	-0.03	0.05	-0.12	-0.12	0.13	-0.24	0.11	0.00	-0.11	-0.21	0.86	0.03	0.05	0.00	-0.17	-0.40	-0.12			
Ca (vol)	0.00	0.07	0.25	-0.24	-0.13	0.13	0.27	-0.36	0.00	0.01	0.26	0.02	-0.04	0.44	0.20	0.19	0.01	0.89	0.40	0.19	-0.17	0.32	0.36	0.05		
Mg (vol)	-0.07	0.28	0.13	0.02	-0.23	0.14	0.06	-0.24	-0.15	-0.05	0.27	-0.11	-0.07	0.51	0.24	0.32	0.07	0.60	0.94	0.43	-0.19	0.43	0.36	-0.03	0.49	
Na (vol)	-0.22	0.29	0.35	-0.22	0.13	-0.21	0.22	0.00	0.00	-0.29	0.25	0.21	-0.18	0.18	0.11	0.18	0.02	0.36	0.36	0.72	0.03	0.25	0.40	0.06	0.39	0.48
K (vol)	0.07	-0.19	0.36	0.09	0.29	-0.13	0.20	-0.03	0.14	-0.12	-0.09	0.41	-0.28	-0.26	-0.13	-0.02	-0.17	-0.22	-0.24	0.04	0.90	-0.25	0.02	-0.14	-0.10	-0.24	0.13

Table 2.6: Correlation matrix from canonical correspondence analysis of the 95 quadrats from the six sites, using all 28 environmental variables.

Figure 2.6: Plot of environmental variables from principal component analysis of all 28 variables in the 95 quadrats (Ca, K, Mg, Na and P = soil nutrient status; S.O.M = organic matter content of soil; F.C = soil moisture content at field capacity; (grav) = results expressed gravimetrically; (vol) = results expressed volumetrically).

CCA was then rerun with these 12 variables removed. The orientation of the resulting biplot (Figures 2.7 and 2.8) was a mirror image of the initial biplot but the quadrats were in similar positions relative to one another and thus the site and TWINSPAN groups have much the same discreteness. Fewer environmental variables resulted in little decrease in the eigenvalues: 0.434 for axis 1 and 0.407 for the second. Furthermore, the Monte Carlo test showed that the removal of these 12 variables did not reduce the significance of the first canonical ordination axis or the trace statistic ($P<0.01$).

Correlations between axes of floristic variation and environmental factors

The most highly correlated variable with the first axis of floristic variation was pH, followed by organic matter content and soil calcium and magnesium (Figure 2.7). On the second axis, soil texture had the highest correlation, followed by soil potassium and sodium. Soil moisture, microtopography and soil structure had significant correlations but were evenly split between the two axes.
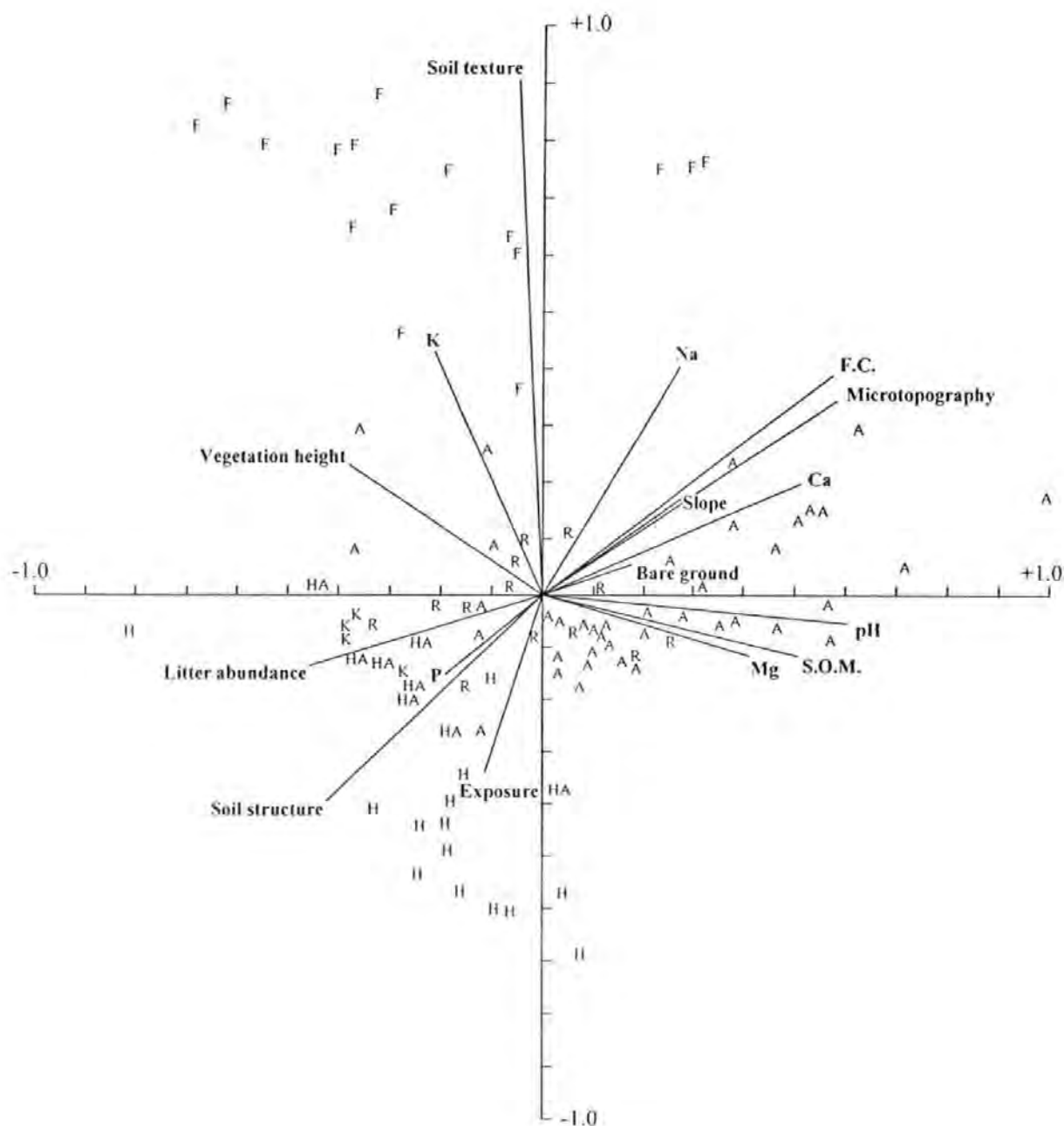
Figure 2.7: Quadrat-environmental biplot from canonical correspondence analysis of the 95 quadrats using the reduced environmental data set (16 variables) with the distribution of the quadrats at the six extant sites superimposed (R = Redlake, A = Andrew's Wood, K = Kilmington, H = Hurst Heath, HA = Hinton Admiral, F = Flimwell) (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity; (grav) = results expressed gravimetrically; (vol) = results expressed volumetrically).
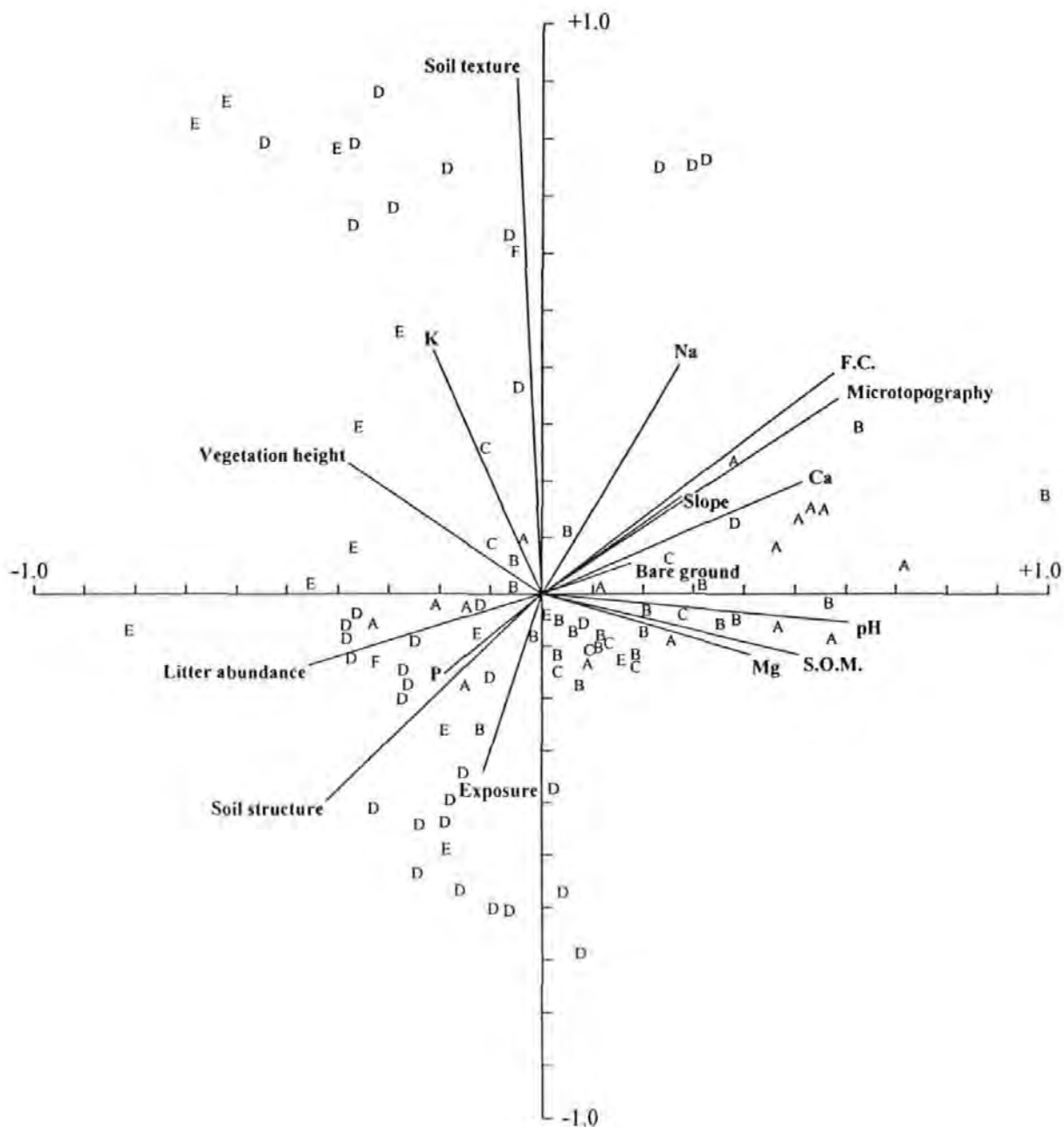
Figure 2.8: Quadrat-environmental biplot from canonical correspondence analysis of the 95 quadrats using the reduced environmental data set (16 variables) with the distribution of TWINSPAN community groups superimposed (Table 2.4) (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity; (grav) = results expressed gravimetrically; (vol) = results expressed volumetrically).

Distribution of the six sites on the quadrat ordination diagram (Figure 2.7)

The quadrats of each of the six sites formed quite distinct groups with little overlap (Figure 2.7 and Tables 2.4 and 2.5). Those from Andrew's Wood, Devon (A) exhibited the widest variation, since it had the largest area and the most sampling. Nevertheless, they were distributed almost entirely to the right centre of the plot. The quadrats from Redlake, Cornwall (R) were largely contained within the distribution of Andrew's Wood, showing they were very similar sites, although the centroid of the cluster had a higher first axis co-ordinate reflecting higher swards, areas of steeper ground and higher available soil phosphorus at Redlake.

The four quadrats from Kilmington, Devon (K) formed a close group characterised by low percentage bare ground, high litter abundance and flat terrain, coupled with acid soils and lower soil moisture content.

The group from Hurst Heath, Dorset (H) lay in a fairly tight group to the lower left of Figure 2.6, indicating lower pH, less bare ground and low relief, both in terms of slope and micro-topography, compared to Andrew's Wood and Redlake. The soil of Hurst Heath contains a greater proportion of sand and is more acidic.

Quadrats from Flimwell, Sussex (F) formed a clear group in the upper left and centre of the plot. The high clay content of soil is important at this site and is reflected in the importance of soil texture on the second axis.

Quadrats from Hinton Admiral, Hampshire (HA) were located towards the left of the first axis, reflecting sandy soil texture, relatively acid soil conditions and high available potassium content combined with low relief, high swards and abundant litter.

The biplot suggested a degree of geographical ordering of the sites (Figure 2.2) along the first axis of the ordination (Figure 2.7) from Flimwell in the east (left of plot) to Redlake and

Andrew's Wood in the west of England (right of plot). The main factors producing this gradient between sites was the variation in soil pH and organic matter content.

Distribution of TWINSPAN groups on the quadrat ordination diagram (Figure 2.8)

Figure 2.8 illustrates the biplot of the quadrats labelled according to the TWINSPAN classification. The six TWINSPAN groups provided a similar pattern of grouping as the sites on the biplot (Figure 2.8). Each group was distinct, yet it met with the next to form a continuum without any separate clusters. Group F contained the two outliers. Groups A, B and C originated from just two sites, at Andrew's Wood (Devon) and Redlake (Cornwall). They formed tighter clusters than groups D and E which had a large spread along the second axis reflecting a wide range of soil textures. Group E quadrats were scattered within woodland/scrub communities (Table 2.4) and were characterised by high swards, abundant litter and an acid soil with a low organic content but with high concentrations of available potassium (Table 2.3). *L. urens* is not generally a member of this community type although it was present at quadrats 81 and 16. These were on the edge of woodland/scrub communities, in more open areas.

Group D has the most members and covers virtually the full spread of the second axis, denoting a wide range of soil textures, from the sandy loam at Hinton Admiral to the Sussex clay of Flimwell (Table 2.3; Figure 2.8). The group is, however, limited to the left-hand side of the biplot, differentiating it from groups A, B and C in terms of soil pH: group D consisted largely of quadrats from the eastern sites of Flimwell, Hinton Admiral and Hurst Heath, whose soils were more acidic than those of Andrew's Wood and Redlake, which made up groups A, B and C, that were situated on the right of the biplot (Table 2.3). Group C included some of the most wooded quadrats from these two sites and hence the group had characteristics similar to group E and was situated closest to it on the biplot.

Two quadrats were allocated to each community which contained *L. urens* (section 2.3.1) (e.g. quadrats 73 & 74, Figure 2.3). To investigate the direct effect of the environment upon the

abundance of *L. urens* the biplot of quadrats was labelled according to *L. urens* abundance (Figure 2.8). The location of the *L. urens* quadrats was not distinct from those quadrats without *L. urens*, the two were inter-dispersed. The connections between community pairs showed no directional trends across all six of the sites but the pairs were generally close together.
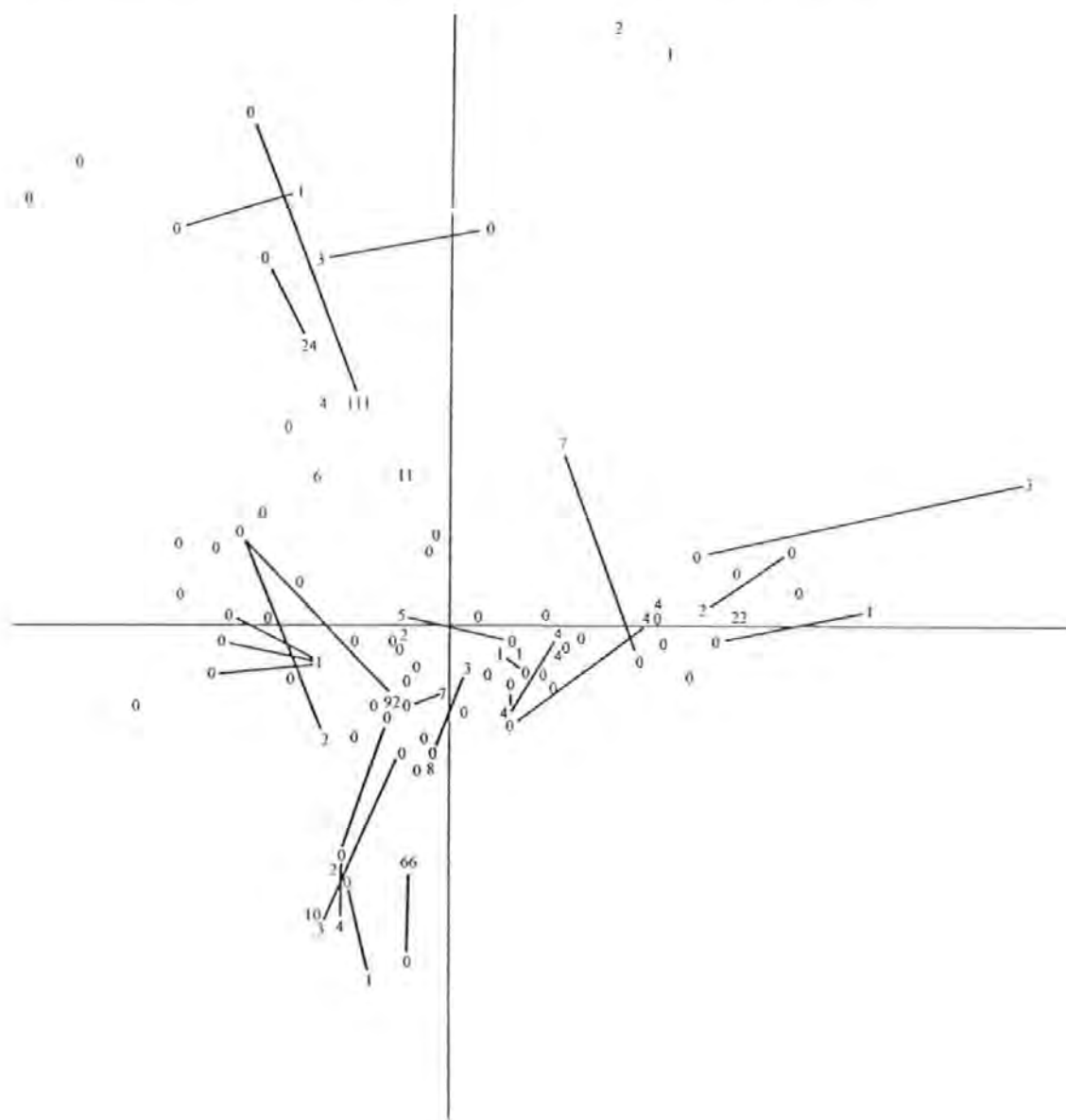
Figure 2.9: Quadrat biplot from canonical correspondence analysis of the 95 quadrats using the reduced data set (16 variables) with the *L. urens* abundance superimposed and the pairs of quadrats within the same communities connected (numbers denote number of *L. urens* plants per quadrat).

2.5.2 *Local analyses*

The classification groups resulting from the TWINSPAN (TSA) analyses are shown in Tables 2.7, 2.9, 2.11, 2.13 & 2.15. CCAs were run using the reduced environmental data set (16 variables), omitting variables from sites where they were homogenous. Quadrat-environmental biplots are shown in Figures 2.11, 2.13, 2.15, 2.17 & 2.19.

Redlake, Cornwall (13 quadrats).

The Redlake quadrats were all classified into groups A and B; the rough grassland M25-dominated communities (Table 2.4). The individual site TWINSPAN analysis (Table 2.7) identified group *v* on the first division, those quadrats, 1, 4, and 6, on the drier banks with a softer grass/scrub community. Group *v* were restricted to the right of the quadrat biplot (Figure 2.11), since they were on steeply sloping ground with low soil moisture content. Percentage soil moisture was positively correlated with micro-topography at Redlake (Table 2.8); dry ground is less susceptible to poaching by grazing animals. *L. urens* was not a member of this community (Table 2.7). Quadrat 5 was singled out to form group *i*, taken on a large bare patch created by a recent bonfire which was dominated by *Lotus uliginosus* and *Juncus conglomeratus*, where no *L. urens* grew (Figure 2.10 & Table 2.7). The remaining quadrats were more similar, all M25 dominated by *Molinia caerulea. Cirsium palustre. Betula pubescens* and *Lotus uliginosus* (Table 2.7). Quadrats 12 and 13, from field 7 (Figure 2.10), were separated from the rest as group *iv* (Table 2.7). The *M. caerulea* was more tussocky in field 7 and thus it provided dry islands separated by wetter furrows in which *Pulicaria dysentrica* and *Succisa pratensis* were present. Figure 2.11 shows that the split between the remaining two communities, groups *ii* and *iii*, was due to soil moisture content. Group *iii* was characterised by *Mentha aquatica* and *Scutellaria minor*, whereas the dominants in group *ii* were *Potentilla erecta* and *Betula pubescens*. *L. urens* was more prominent in the drier of these two communities, namely *ii*. Although the axes of the biplot explain a reasonable amount of the variation present (eigenvalues: axis 1, 0.51; axis 2, 0.36), a large number of the environmental variables examined at Redlake were highly correlated to one another (Table 2.8) and, hence, soil moisture may not have been the only major significant factor differentiating community groups *ii* and *iii*.

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Figure 2.10: Site sketch map with the 13 quadrats at Redlake, Cornwall. The regional and local TWINSPAN (TSA) quadrat groups are indicated.

Species	i	ii	iii	iv	v	Species
Dactylis glomerata	IV 2			IV 2		Dactylis glomerata
Rumex acetosa	IV 2			IV 2		Rumex acetosa
Hypericium androsaenium				IV 2		Hypericium androsaenium
Pulicaria dysentrica				VI 2		Pulicaria dysentrica
Succisa pratensis			III 2	VI 2		Succisa pratensis
Taraxacum officinale agg.				IV 2		Taraxacum officinale agg.
Galium palustre			IV 2	IV 2		Galium palustre
Potentilla erecta		IV 3	IV 2	VI 2		Potentilla erecta
Betula pubescens		IV 3	III 3			Betula pubescens
Circaea lutetiana		III 1				Circaea lutetiana
Dryopteris dilatata		III 2				Dryopteris dilatata
Dryopteris filix-mas		III 2				Dryopteris filix-mas
Lychnis flos-cuculi		III 1				Lychnis flos-cuculi
Ulex europaeus		III 2				Ulex europaeus
Juncus acutiflorus		V 3	IV 4	VI 2		Juncus acutiflorus
Lobelia urens		V 2	III 2	IV 2		Lobelia urens
Salix aurita		V 3	III 3	IV 2		Salix aurita
Deschampsia flexuosa		V 2	V 2			Deschampsia flexuosa
Juncus effusus			III 3			Juncus effusus
Mentha aquatica		III 2	V 2			Mentha aquatica
Polygonum hydropiper			III 1			Polygonum hydropiper
Scutellaria minor			IV 2			Scutellaria minor
Cirsium palustre		V 2	VI 2	IV 2		Cirsium palustre
Juncus conglomeratus	IV 3	V 2	V 2			Juncus conglomeratus
Molinia caerulea			VI 3	VI 3	V 3	Molinia caerulea
Lotus uliginosus	IV 3	V 2	VI 2	VI 3	VI 2	Lotus uliginosus
Rubus fruticosus		V 3	IV 2	VI 2	V 3	Rubus fruticosus
Angelica sylvestris				IV 2	III 2	Angelica sylvestris
Holcus lanatus		III 3		IV 3	V 3	Holcus lanatus
Centaurea nigra		III 1		IV 2	VI 3	Centaurea nigra
Agrostic curtisii		III 3	III 1		V 3	Agrostic curtisii
Agrostis stolonifera					III 3	Agrostis stolonifera
Plantago lanceolata		V 2			VI 3	Plantago lanceolata
Stellaria graminea					III 1	Stellaria graminea

Table 2.7: Species composition of the five community types defined by two-way indicator species analysis of the data from the 13 Redlake, Cornwall quadrats. The first column corresponds to species constancy within each TWINSPAN group (I = 5% or less; II = 6-20%; III = 21-40%; IV = 41-60%; V = 61-80%; VI= 81-100%). The second column indicates average species abundance for each group on the domin scale.

Figure 2.11 Quadrat-environmental biplot from canonical correspondence analysis of Redlake, Cornwall using 15 environmental variables with the distribution of TWINSPAN community groups superimposed (Table 2.7) (Ca, K, Mg, Na and P = soil nutrient status, S.O.M. = organic matter content of soil, F.C. = soil moisture content at field capacity, (grav) = results expressed gravimetrically).

	Slope	Exposure	Vegetation height	Microtopography	Litter abundance	Bare ground	Soil structure	pH	S.O.M.	F.C.	P	Ca	Mg	Na
Exposure	-0.95													
Vegetation height	-0.17	0.21												
Microtopography	-0.63	0.72	0.63											
Litter abundance	-0.58	0.55	0.17	0.29										
Bare ground	-0.08	0.08	0.12	-0.17	0.18									
Soil structure	0.61	-0.68	-0.39	-0.78	-0.43	-0.04								
pH	0.17	0.18	-0.13	-0.10	0.33	0.53	0.22							
S.O.M.	0.23	0.35	0.30	0.35	-0.03	-0.16	-0.27	-0.06						
F.C.	-0.70	0.78	0.49	0.89	0.35	-0.24	-0.75	-0.21	0.55					
P	0.38	-0.49	-0.10	-0.45	0.22	0.29	0.47	0.17	-0.25	-0.33				
Ca	-0.30	0.18	0.10	0.12	0.00	0.41	0.10	0.56	-0.15	-0.02	0.33			
Mg	-0.11	0.09	0.17	0.23	0.29	-0.01	0.14	0.38	-0.15	0.20	0.37	0.55		
Na	-0.52	0.43	0.35	0.40	0.43	0.28	-0.21	0.24	-0.24	0.36	0.21	0.69	0.71	
K	-0.15	0.17	0.78	0.60	0.23	-0.09	-0.57	-0.45	0.14	0.52	-0.16	-0.12	0.06	0.37

Table 2.8: Correlation matrix from canonical correspondence analysis of data from 13 Redlake, Cornwall quadrats using 15 environmental variables (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity, (grav) = results expressed gravimetrically).

Andrew's Wood, Devon (40 quadrats).

Three major plant community types were identified at Andrew's Wood (Figure 2.12). The first, classified as group *iv* (Table 2.9) and within group C (Table 2.4), was that of recently cleared woodland or scrub which was characterised by a combination of woodland features: an impoverished ground flora dominated by *Rubus fruticosus* and *Lonicera periclymenum* (Table 2.9) and a high proportion of bare ground, with the low soil organic matter content typical of disturbed ground (Figure 2.13). *L. urens* is not generally a member of this H4 - *Ulex gallii-Agrostis curtisii* heath community type (Table 2.9). *Molinia caerulea* dominated the remaining two communities. One community, group *ii* (quadrats 17-24, 27+28, 32-35, 43+44)(Table 2.9), classified largely within group B (Table 2.4), having *Potentilla erecta, Angelica sylvestris* and *Cirsium palustre* as co-dominants, was strictly M25c - *Molinia caerulea-Potentilla erecta*, sub-community *Angelica sylvestris*. The second community, group *i* (Table 2.9), encompassed a more diverse group of quadrats which occurred in the southern areas of fields D and C3 (i.e. quadrats 29, 36-38, 45-53). This community was a cross between a M23 - *Juncus effusus/acutiflorus-Galium palustre* rush-meadow and a M24 - *Molinia caerulea-Cirsium dissectum* fen-meadow, with no *Potentilla erecta*, and little *Angelica sylvestris*. Instead, the co-dominants were *Pulicaria dysenterica, Juncus articulatus* and *Rubus fruticosus*. Figure 2.13 shows that these two plant communities were separated on the basis of calcium availability in the soil, closely correlated with soil pH and moisture content, and the abundance of litter on the soil surface (Figure 2.13). *L. urens* was scattered through both of these communities. Group *iii* consisted of quadrats 39 and 40 (Table 2.9) which were both outliers brought together by virtue of their tall swards (Figure 2.13); quadrat 39 was beneath bracken and quadrat 40 was an area which was cleared from woodland a couple of years ago (Figure 2.12). These two quadrats were as species poor and as bare as those of the recently cleared woodland, group *iv*, but did not contain of the same shade-tolerant *Lonicera periclymenum* and *Rubus fruticosus* (Table 2.9). Quadrat 40 had a high *L. urens* abundance (Table 2.9).
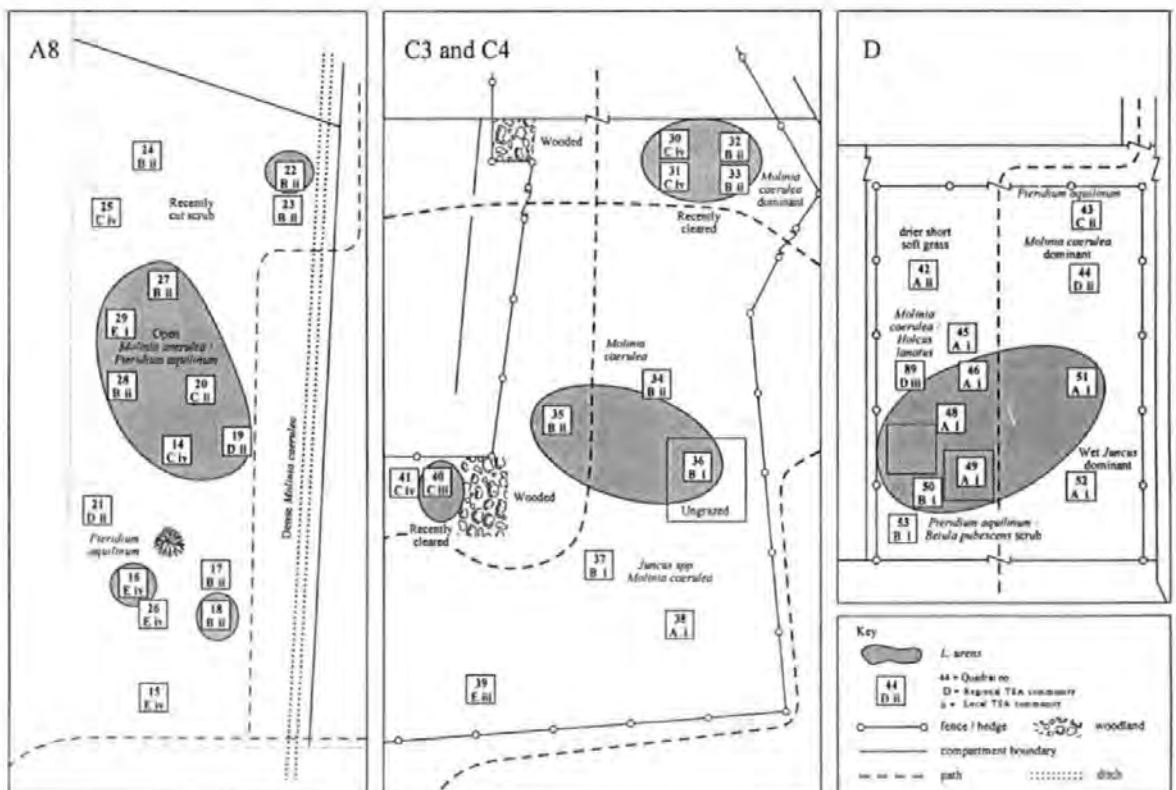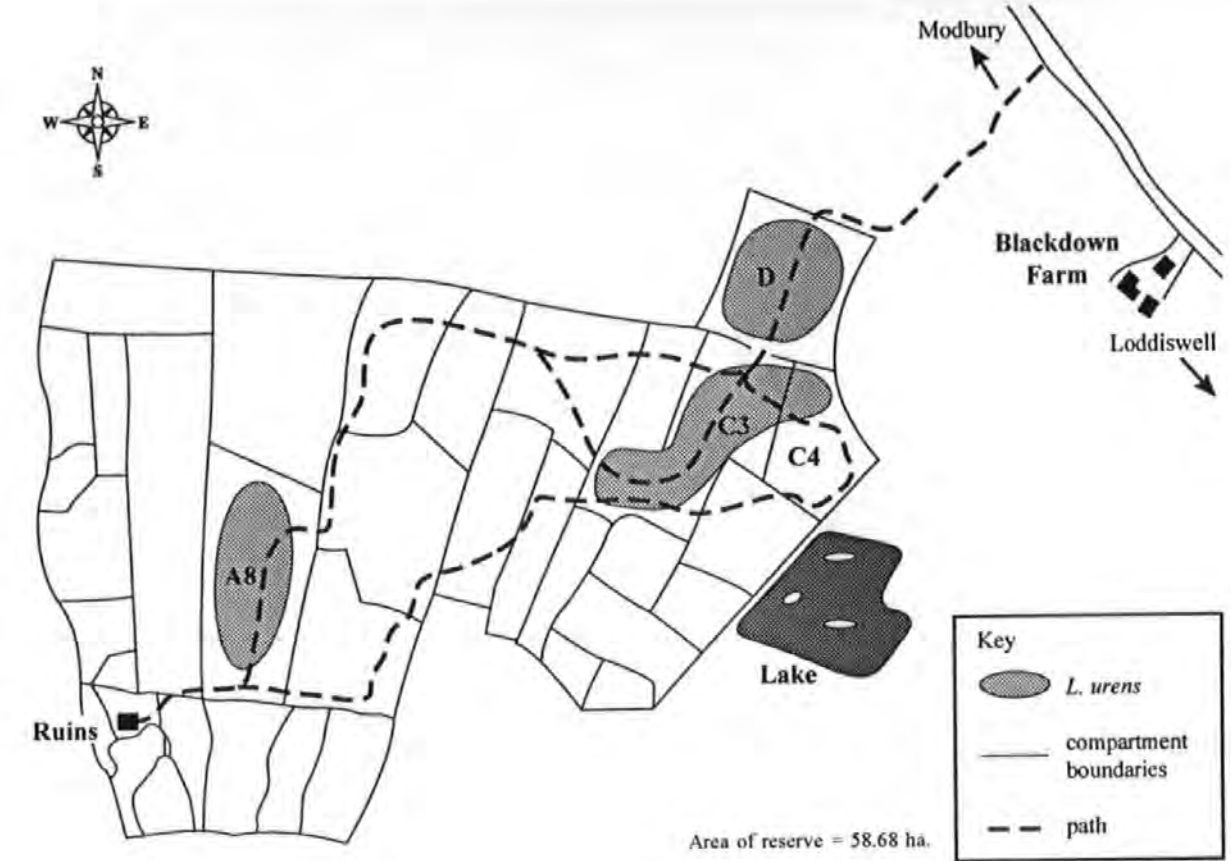
Figure 2.12: Site sketch maps with the 40 quadrats of Andrew's Wood, Devon. The regional and local TWINSPAN (TSA) quadrat groups are indicated. The large squares in compartments C and D are grazing exclosures.

Twinspan group

Species	i	ii	iii	iv	Species
Juncus bufonius	III 3	II 2		II 2	*Juncus bufonius*
Mentha aquatica	IV 2	III 2	V 2	II 2	*Mentha aquatica*
Juncus articulatus	IV 3	III 2		II 2	*Juncus articulatus*
Ajuga reptans	I 2	+ 1			*Ajuga reptans*
Carex hostiana	I 3				*Carex hostiana*
Dactylorhiza praetermissa	I 2				*Dactylorhiza praetermissa*
Epilobium montanum	I 2		V 1		*Epilobium montanum*
Geranium robertanium	I 2		V 1		*Geranium robertanium*
Hydrocotyle vulgaris	II 3				*Hydrocotyle vulgaris*
Lotus uliginosus	II 2	I 3			*Lotus uliginosus*
Plantago lanceolata	III 2	I 3			*Plantago lanceolata*
Pulicaria dysenterica	V 2	II 2			*Pulicaria dysenterica*
Ranunculus acris	I 2				*Ranunculus acris*
Stellaria alsine	I 2	I 2			*Stellaria alsine*
Anagallis tenella	I 2				*Anagallis tenella*
Callitriche stagnalis	I 3				*Callitriche stagnalis*
Carduus crispus	I 2				*Carduus crispus*
Centaurea nigra	II 2				*Centaurea nigra*
Dactylorhiza maculata	I 2				*Dactylorhiza maculata*
Filipendula ulmaria	I 3				*Filipendula ulmaria*
Luzula campestris	I 2				*Luzula campestris*
Ranunculus ficaria	I 2				*Ranunculus ficaria*
Ranunculus flammula	II 2				*Ranunculus flammula*
Rumex acetosa	I 2				*Rumex acetosa*
Veronica scutellata	I 1				*Veronica scutellata*
Molinia caerulea	V 3	VI 3	V 3	II 3	*Molinia caerulea*
Holcus lanatus	IV 2	IV 3			*Holcus lanatus*
Lotus corniculatus	I 2	+ 3			*Lotus corniculatus*
Lysimachia nemorum	I 2		VI 2		*Lysimachia nemorum*
Plantago major	I 2	I 2			*Plantago major*
Salix aurita	I 2	+ 3			*Salix aurita*
Taraxacum offiniale agg.	I 1	+ 2			*Taraxacum offiniale agg.*
Cirsium palustre	IV 2	V 2			*Cirsium palustre*
Fragaria vesca		+ 1	V 3		*Fragaria vesca*
Ranunculus repens	I 2		VI 3		*Ranunculus repens*
Solanum dulcamara			V 2		*Solanum dulcamara*
Ulex europaeus			V 2		*Ulex europaeus*
Carex echinata		I 2			*Carex echinata*
Leontodon hispidus		+ 1			*Leontodon hispidus*
Epilobium hirsutum		+ 1			*Epilobium hirsutum*
Erica tetralix		I 2			*Erica tetralix*
Urtica dioica		+ 2			*Urtica dioica*
Viburnum opulus		+ 3			*Viburnum opulus*
Achillea millefolium		+ 3			*Achillea millefolium*
Achillea ptarmica		+ 1			*Achillea ptarmica*
Poa trivialis		I 2			*Poa trivialis*
Prunella vulgaris		+ 2			*Prunella vulgaris*
Quercus robur		+ 3			*Quercus robur*
Deschampsia flexuosa		+ 3			*Deschampsia flexuosa*
Festuca rubra		V 3			*Festuca rubra*
Hypericum pulchrum		I 1			*Hypericum pulchrum*
Succisa pratensis		I 2			*Succisa pratensis*
Potentilla erecta	I 2	VI 2		II 1	*Potentilla erecta*
Angelica sylvestris	IV 2	VI 2		III 2	*Angelica sylvestris*
Betula pubescens	II 2	IV 2	V 1	III 2	*Betula pubescens*
Juncus conglomeratus	I 2	III 3	V 2	II 4	*Juncus conglomeratus*
Pteridium aquilinum	I 1	III 2	V 4	II 2	*Pteridium aquilinum*
Lobelia urens	IV 2	II 2	V 3	II 2	*Lobelia urens*
Galium palustre	I 2	II 2		III 2	*Galium palustre*
Viola palustre	I 1	III 2	V 1	IV 2	*Viola palustre*
Hedera helix	I 1		V 2	IV 1	*Hedera helix*
Veronica montana			V 1	II 2	*Veronica montana*
Stachys officinalis				II 2	*Stachys officinalis*
Hypericum tetrapterum				II 2	*Hypericum tetrapterum*
Lamium purpureum				II 2	*Lamium purpureum*
Lonicera periclymenum		+ 2		IV 2	*Lonicera periclymenum*
Teucrium scorodonia		+ 1		III 3	*Teucrium scorodonia*
Athyrium filix-femina				II 2	*Athyrium filix-femina*
Dryopteris filix-mas				II 3	*Dryopteris filix-mas*
Rubus fruticosus	IV 2	II 1		VI 2	*Rubus fruticosus*
Salix cinerea	I 3	I 2		II 3	*Salix cinerea*

Table 2.9: Species composition of the four community types defined by two-way indicator species analysis of the data from the 40 Andrew's Wood, Devon quadrats. The first column corresponds to species constancy within each TWINSPAN group (I = 5% or less; II = 6-20%; III = 21-40%; IV = 41-60%; V = 61-80%; VI= 81-100%). The second column indicates average species abundance for each group on the domin scale
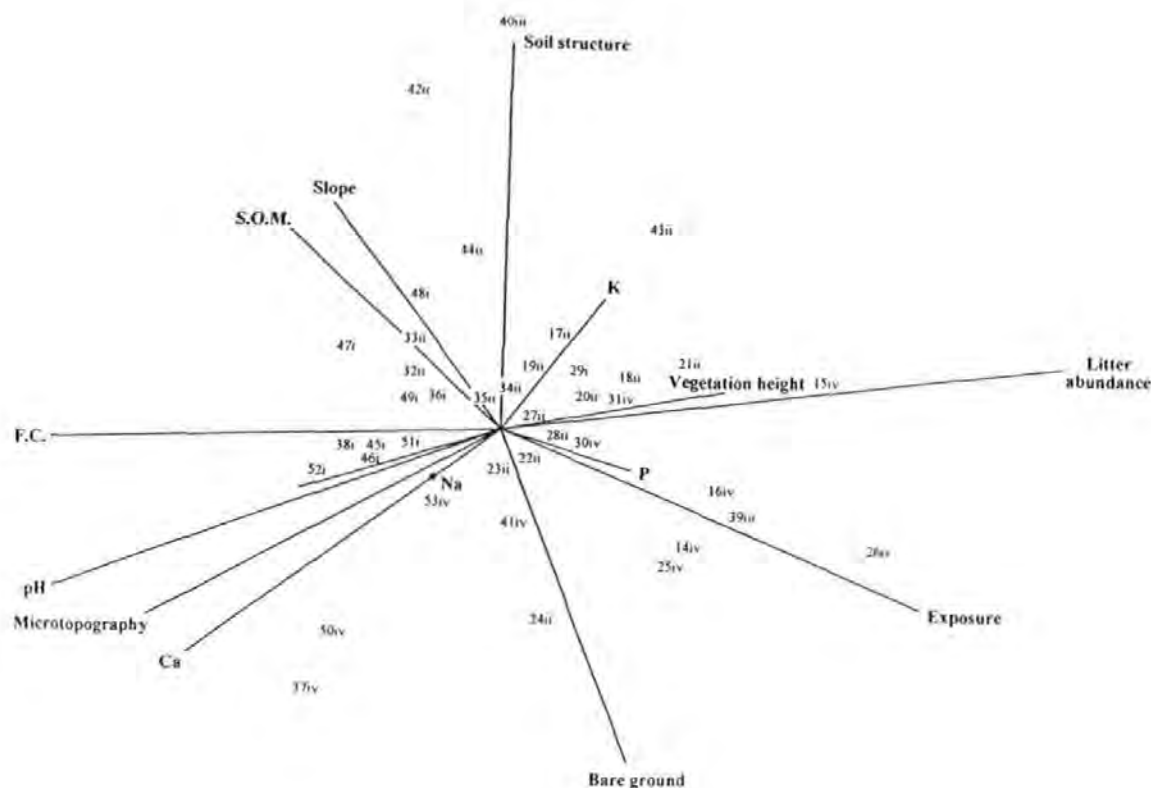
Figure 2.13 Quadrat-environmental biplot from canonical correspondence analysis of the 40 quadrats at Andrew's Wood, Devon using 15 environmental variables with the distribution of TWINSPAN community groups superimposed (Table 2.9) (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity)

	Slope	Exposure	Vegetation height	Microtopography	Litter abundance	Bare ground	Soil structure	pH	S.O.M	F.C	P	Ca	Mg	Na
Exposure	-0.39													
Vegetation height	-0.15	-0.09												
Microtopography	0.33	-0.43	-0.21											
Litter abundance	-0.00	0.46	0.35	-0.34										
Bare ground	0.03	0.08	0.13	0.12	0.22									
Soil structure	-0.08	-0.21	0.16	-0.37	0.06	-0.06								
pH	0.06	-0.42	0.01	0.28	-0.51	0.06	0.14							
S.O.M	0.16	-0.43	0.04	0.01	-0.11	-0.26	0.43	0.43						
F.C	0.13	-0.56	-0.05	0.31	-0.39	0.12	0.18	0.62	0.60					
P	-0.13	0.19	0.11	-0.07	0.22	0.17	0.10	0.09	-0.07	-0.13				
Ca	0.29	-0.33	-0.04	0.43	-0.34	0.05	-0.06	0.57	0.35	0.38	-0.03			
Mg	-0.00	0.06	-0.02	-0.03	-0.29	0.01	0.02	0.41	0.31	0.40	-0.03	0.33		
Na	0.33	-0.17	0.21	0.08	-0.03	0.23	-0.04	0.32	0.35	0.38	0.14	0.29	0.51	
K	-0.14	-0.01	-0.02	-0.08	-0.07	-0.07	-0.03	-0.33	-0.18	-0.13	-0.10	-0.17	-0.08	-0.03

Table 2.10: Correlation matrix from canonical correspondence analysis of the 40 Andrew's Wood, Devon quadrats using 15 environmental variables (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity).

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Kilmington, Devon (4 quadrats).

An individual analysis of this site was not possible since only four quadrats were sampled.

Hurst Heath, Dorset (14 quadrats).

The first two axes on the individual site biplot (Figure 2.15) accounted for 77% and 64% respectively of the variation present within the Hurst Heath data. All but two of the Hurst Heath quadrats were classified into group D (Table 2.4). A small area of Hurst Heath was rotovated, thus maintaining an open sward to help to sustain the *L. urens* population (see section 2.2). Data were collected in and around this rotovated patch (Figure 2.14). Groups *i*, *ii* and *v* (Table 2.11) were all situated either on the edge of the rotovated area or outside within the *Pinus-Betula* mixed woodland. Quadrat 71 was singled out as group *v*, since it occurred in an area dominated by *Pteridium aquilinum* (Table 2.11) which consequently had a modified soil, being more acidic and with a greater proportion of organic matter (Table 2.12) and a stronger structure (Figure 2.15). Quadrats 69 and 70, group *ii*, were species-poor quadrats beneath woodland, dominated by *Molinia caerulea* but with no *L. urens* (Table 2.11). Quadrats 64 and 67, group *i*, occurred on the wettest edge of the disturbed plot and represented communities similar to the M25 of Andrew's Wood and Redlake. *Salix repens* had invaded and formed a tall sward in conjunction with other species common to wetland such as *Juncus conglomeratus*, *Juncus acutiflorus*, *Eupatorium cannabinum* and *Hypericum undulatum* (Figure 2.14 & Table 2.11). The remaining quadrats were all much more heathy - H3, *Ulex minor-Agrostis curtisii* heath. They were largely contained within the cultivated plot, and were split on the basis of time since last disturbance. Quadrats 62 and 63, within group *iii*, were rotovated in the winter of 1992 (Figure 2.14). The group was characterised by *Veronica chamedrys* and *Viola lactea* (Table 2.11). Group *iv* (quadrats 58-61, 65, and 68) occurred in the areas which were open but had not been subjected to recent disturbance, and where heath species *Erica tetralix* and *Ulex minor* had established. *L. urens* was restricted mainly to the cultivated plot with large numbers of plants established in the sections rotovated in 1986 (group *iv*). However, a few plants did survive in clearings within the woodland e.g. quadrat 68 (Table 2.11).
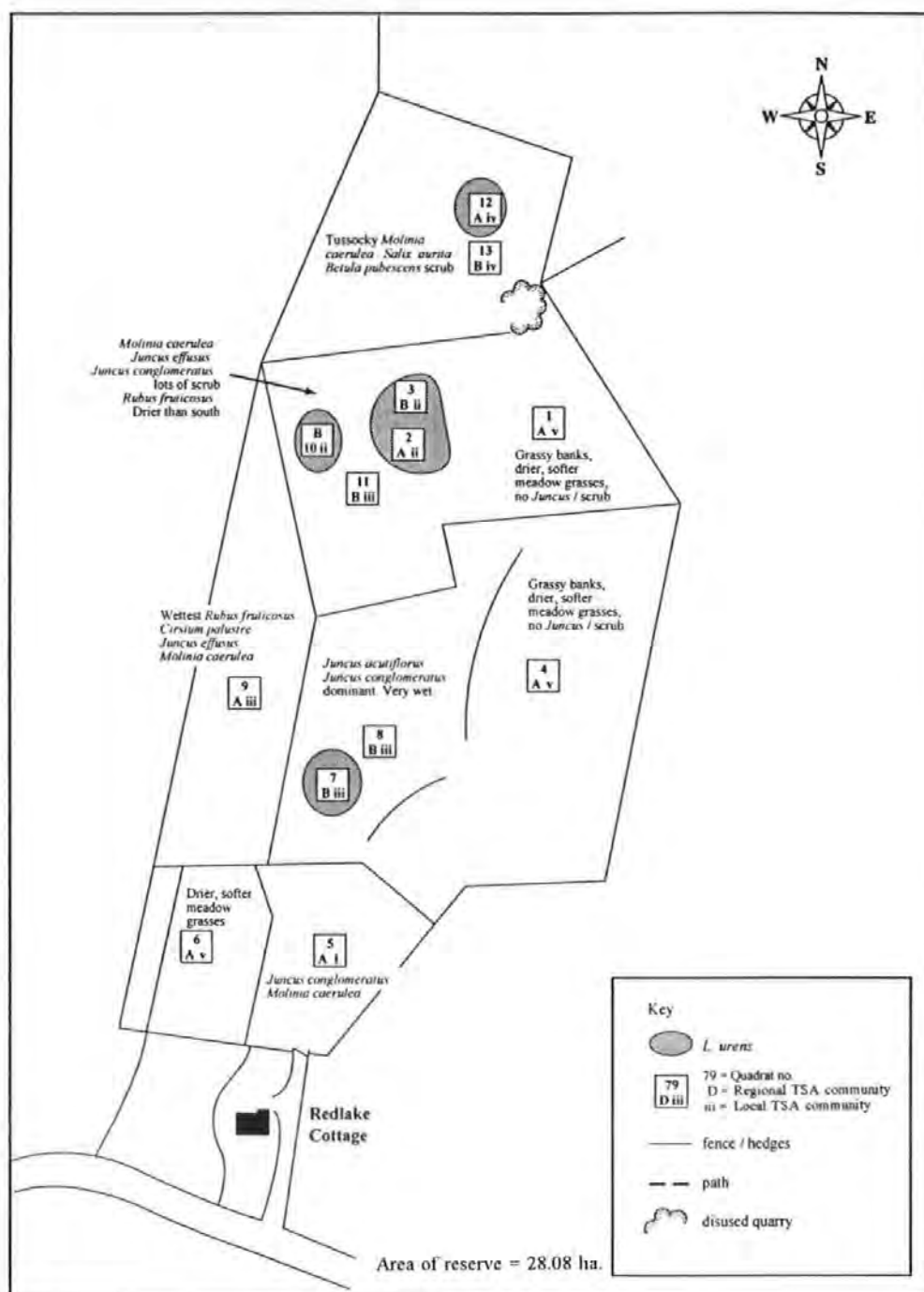
Figure 2.14: Site sketch map with the 14 quadrats of Hurst Heath, Dorset. The regional and local TWINSPAN (TSA) quadrat groups are indicated.

Twinspan group

Species	i	ii	iii	iv	v	Species
Scutellaria minor	VI 2		V 2			Scutellaria minor
Cirsium palustre	IV 2					Cirsium palustre
Eupatorium cannabinum	IV 3					Eupatorium cannabinum
Hypericum undulatum	IV 1					Hypericum undulatum
Juncus acutiflorus	VI 2					Juncus acutiflorus
Juncus conglomeratus	IV 2					Juncus conglomeratus
Lysimachia nemorum	IV 3					Lysimachia nemorum
Salix repens	IV 2					Salix repens
Carex binervis	IV 2		V 2	II 1		Carex binervis
Lobelia urens	IV 2	VI 4	III 2	V 2		Lobelia urens
Molinia caerulea	VI 3	VI 2	V 3	VI 3		Molinia caerulea
Potentilla erecta	VI 3	IV 2	VI 3	VI 3		Potentilla erecta
Lonicera periclymenum						Lonicera periclymenum
Agrostis curtsii			III 3			Agrostis curtsii
Angelica sylvestris			III 1			Angelica sylvestris
Hypericum pulchrum			III 2			Hypericum pulchrum
Hypochoeris glabra			III 1			Hypochoeris glabra
Veronica chamaedrys			VI 1			Veronica chamaedrys
Viola lactea			V 2	II 2		Viola lactea
Festuca rubra			III 2	II 2		Festuca rubra
Hieracium pilosella			III 3	III 2		Hieracium pilosella
Taraxacum officinale agg.			III 2	III 2		Taraxacum officinale agg.
Rubus fruticosus			V 2	V 2		Rubus fruticosus
Danthonia decumbens			III 3	III 3		Danthonia decumbens
Viola riviniana			III 2	V 2		Viola riviniana
Centaurea nigra				IIIII 2		Centaurea nigra
Genista angelica				III 2		Genista angelica
Luzula multiflora				II 1		Luzula multiflora
Prunella vulgaris				II 2		Prunella vulgaris
Ulex minor				V 2		Ulex minor
Carex flacca				II 2		Carex flacca
Crepis biennis				VI 1		Crepis biennis
Erica tetralix				V 3		Erica tetralix
Galium palustre				III 3		Galium palustre
Cirsium dissectum			III 1	V 2		Cirsium dissectum
Betula pubescens		IV 2	III 1	II 1	VI 3	Betula pubescens
Hedera helix					VI 3	Hedera helix
Pteridium aquilinum				III 2	VI 4	Pteridium aquilinum

Table 2.11: Species composition of the five community types defined by two-way indicator species analysis of the data from the 14 Hurst Heath, Dorset quadrats. The first column corresponds to species constancy within each TWINSPAN group (I = 5% or less; II = 6-20%; III = 21-40%; IV = 41-60%; V = 61-80%; VI= 81-100%). The second column indicates average species abundance for each group on the domin scale.
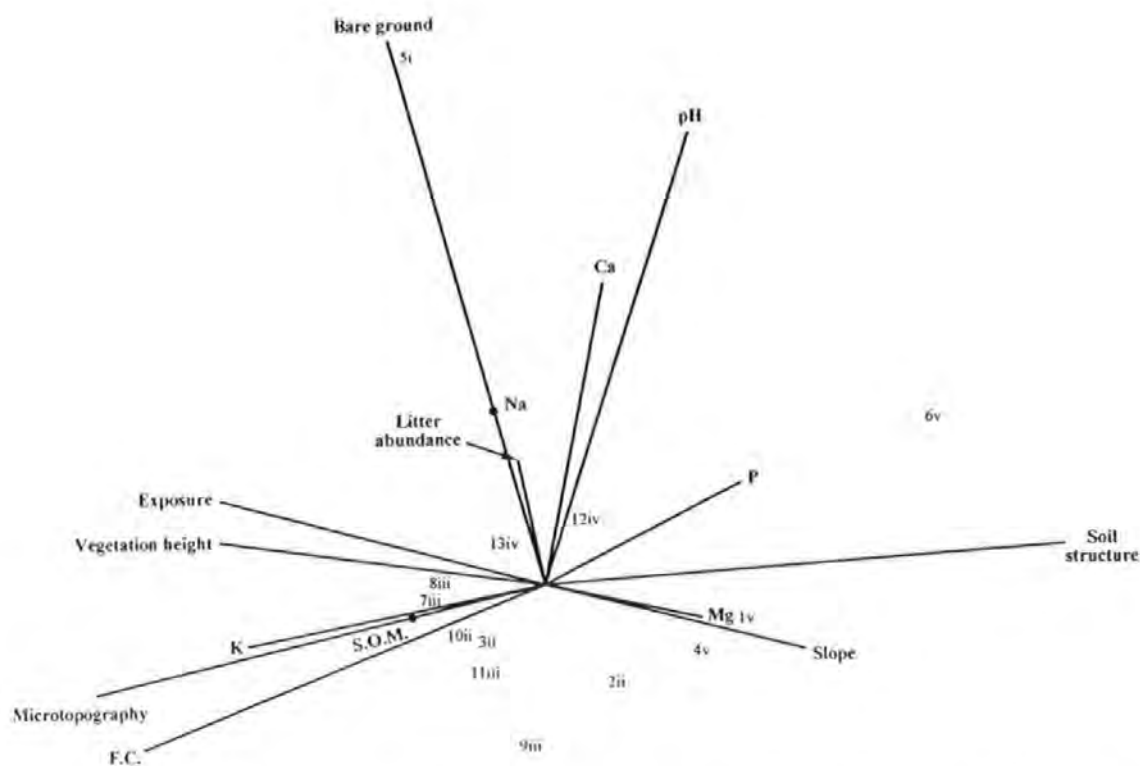
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Figure 2.15: Quadrat-environmental biplot from canonical correspondence analysis of 14 quadrats at Hurst Heath, Dorset using 14 environmental variables with the distribution of TWINSPAN community groups superimposed (Table 2.11) (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity).

	Vegetation height	Microtopography	Litter abundance	Bare ground	Soil texture	Soil structure	pH	S.O.M.	F.C.	P	Ca	Mg	Na
Microtopography	-0.16												
Litter abundance	0.72	0.10											
Bare ground	-0.71	0.44	-0.24										
Soil texture	0.13	0.47	0.52	0.21									
Soil structure	0.28	-0.61	0.15	-0.27	-0.11								
pH	-0.47	-0.10	-0.66	0.26	-0.38	-0.37							
S.O.M.	0.13	0.04	0.32	-0.14	0.27	0.36	-0.76						
F.C.	0.44	-0.09	0.15	-0.61	-0.24	0.09	-0.07	-0.10					
P	-0.24	0.60	-0.10	0.55	0.47	-0.43	0.23	-0.10	-0.62				
Ca	-0.08	-0.06	-0.25	0.10	-0.30	-0.18	0.63	-0.32	0.10	0.24			
Mg	-0.43	-0.17	-0.40	0.36	-0.17	-0.16	0.76	-0.27	-0.22	0.27	0.77		
Na	0.36	-0.33	0.54	0.12	0.19	0.49	-0.22	0.14	-0.20	0.03	0.29	0.18	
K	-0.19	-0.36	0.02	0.15	-0.25	0.05	-0.10	0.01	-0.39	-0.30	-0.17	-0.07	0.26

Table 2.12: Correlation matrix from canonical correspondence analysis of data from 14 Hurst Heath, Dorset quadrats using 14 environmental variables (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity).

Hinton Admiral, Hampshire (8 quadrats).

L. urens was found within a heath community dominated by *Molinia caerulea* and *Potentilla erecta* at Hinton Admiral (Figure 2.16). Quadrats 73, 74, 75 and 77, group *ii* (Table 2.13), represented this rough grassland community and were classified thus in the overall TWINSPAN (Table 2.4). Quadrats 72, 76, and 78, group *iii*, corresponded to a scrubland community dominated by *Calluna vulgaris, Ulex europeaus* and *Rubus fruticosus* (Table 2.13). Quadrat 79 was singled out in the local analysis to form group *i*, as it was situated in a dense, grassy sward, dominated by *Agrostis* spp.. However, quadrat 79 was not separated from the main grassland community, group *ii*, in the regional analysis (Table 2.4). The two major plant communities of Hinton Admiral, grassland and scrubland, were distinct in terms of their environment. Figure 2.17 shows the grassland community on the left, characterised by a short sward, which was strongly correlated with a number of other variables, including pH, and the concentration of P, Na, and Ca in the soil (Table 2.14).
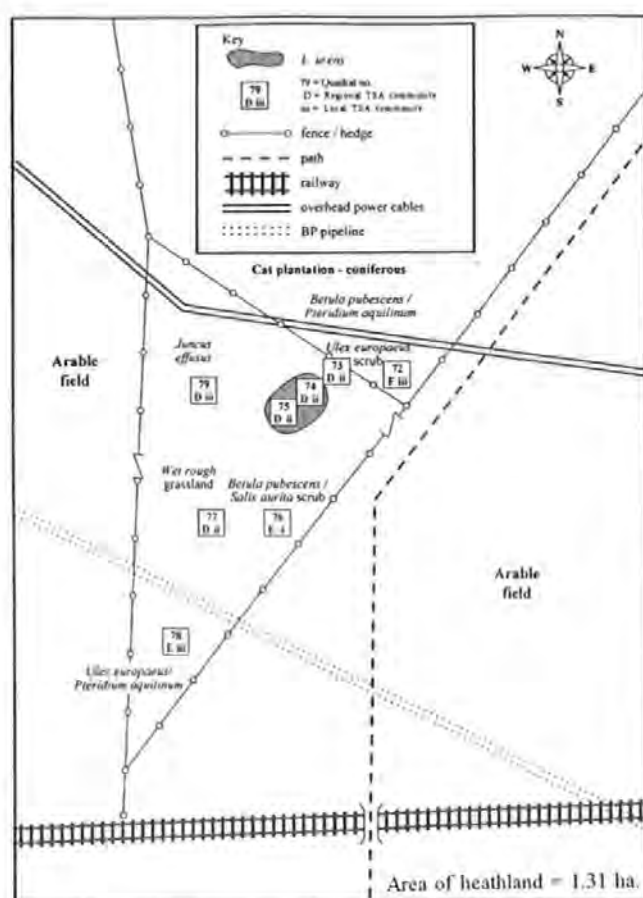
Figure 2.16: Site sketch map with the 8 quadrats of Hinton Admiral, Hampshire. The regional and local TWINSPAN (TSA) quadrat groups are indicated.

| | Twinspan group | | | |
Species	i	ii	iii	Species
Anthoxanthum odoratum		IV 3		*Anthoxanthum odoratum*
Centaurium erythræa		III 2		*Centaurium erythræa*
Cirsium dissectum		III 2		*Cirsium dissectum*
Erica cinerea		III 3		*Erica cinerea*
Erica tetralix		III 3		*Erica tetralix*
Hypericum pulchrum		III 2		*Hypericum pulchrum*
Hypochoeris radicata		III 3		*Hypochoeris radicata*
Lobelia urens		IV 3		*Lobelia urens*
Lotus ulinginosus		III 2		*Lotus ulinginosus*
Potentilla erecta		V 3		*Potentilla erecta*
Rosa canina		III 2		*Rosa canina*
Rumex acetosella		IV 2		*Rumex acetosella*
Agrostis capillaris	VI 2			*Agrostis capillaris*
Agrostis curtsii	VI 3			*Agrostis curtsii*
Juncus effusus	VI 2	III 3		*Juncus effusus*
Molinia caerula	VI 2	VI 3	III 3	*Molinia caerula*
Rubus fruticosus		III 2	V 3	*Rubus fruticosus*
Teucrium scorodonia	VI 2		III 2	*Teucrium scorodonia*
Calluna vulgaris			V 3	*Calluna vulgaris*
Pteridium aquilinum			III 3	*Pteridium aquilinum*
Quercus robur			III 3	*Quercus robur*
Salix aurita			III 3	*Salix aurita*
Ulex europaeus			V 3	*Ulex europaeus*

Table 2.13: Species composition of the three community types defined by two-way indicator species analysis of the data from the 8 Hinton Admiral, Hampshire quadrats. The first column corresponds to species constancy within each TWINSPAN group (I = 5% or less; II = 6-20%; III = 21-40%; IV = 41-60%; V = 61-80%; VI= 81-100%). The second column indicates average species abundance for each group on the domin scale.

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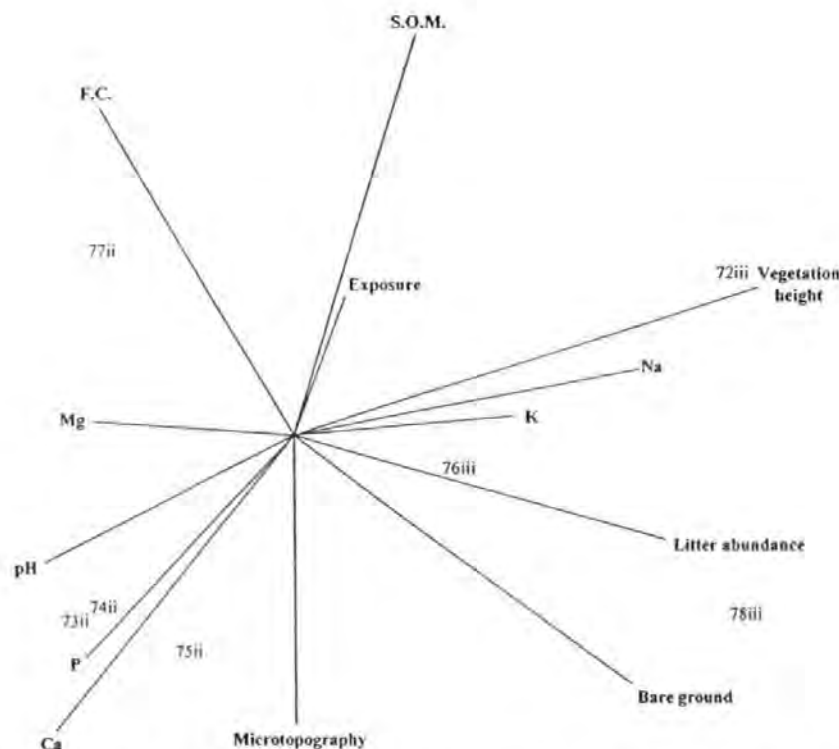
Figure 2.17: Quadrat-environmental biplot from canonical correspondence analysis of the 8 quadrats from Hinton Admiral, Hampshire using 13 environmental variables with the distribution of TWINSPAN community groups superimposed (Figure 2.13b) (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity).

	Exposure	Vegetation height	Microtopography	Litter abundance	Bare ground	pH	S.O.M.	F.C.	P	Ca	Mg	Na
Sward height	0.09											
Microtopography	0.53	-0.18										
Litter abundance	0.04	0.36	0.34									
Bare ground	0.40	0.61	0.35	0.63								
pH	-0.21	-0.16	0.28	0.07	-0.45							
S.O.M	-0.17	0.46	-0.50	0.44	0.02	-0.04						
F.C.	0.52	0.06	-0.20	-0.09	0.11	-0.13	0.35					
P	-0.08	-0.64	0.04	-0.17	-0.20	0.58	-0.35	0.24				
Ca	-0.14	-0.62	0.27	-0.49	-0.35	0.42	-0.60	-0.54	0.12			
Mg	0.16	0.16	-0.34	-0.25	0.25	-0.21	0.23	0.48	-0.06	0.10		
Na	0.01	0.82	-0.49	0.35	0.62	-0.59	0.49	0.31	-0.19	-0.59	0.49	
K	0.44	0.47	-0.22	-0.28	0.44	-0.66	-0.20	0.29	-0.07	-0.09	0.49	0.60

Table 2.14: Correlation matrix from canonical correspondence analysis of data from 8 Hinton Admiral, Hampshire quadrats using 13 environmental variables (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity).

Flimwell, Sussex (16 quadrats).

Traditionally this site was managed as a sweet-chestnut coppice, which produced two major communities; the mature chestnut woodland and open areas such as rides and recently cut sections; *L. urens* was a member of the latter community type (see section 2.2). The mature chestnut woodland community still exists (Figure 2.18), as represented by quadrats 81, 82, 84 and 85 which formed group *i* (Table 2.15) and were part of the woodland community group E (Table 2.4). This community was characterised by an impoverished ground flora and was dominated by *Castanea sativa, Rubus fruticosus* and *Betula pubescens*. It did not contain *L. urens* (Table 2.15). In Figure 2.19 these woodland quadrats form a distinct group, having a high percentage litter cover, closely correlated with high soil organic matter content (Table 2.16), coupled with a high proportion of bare ground and even surface. The original community for *L. urens* at Flimwell; disturbed, open areas within the chestnut woodland, has been enlarged recently by the development of a bird park (see section 2.2). Group *ii*, (quadrats 80, 81, 83, 86, 93 and 94), which were taken from within and around the edge of the bird park (Figure 2.14a),

represented this original *L. urens* community, a relatively species rich M25 community dominated by *Juncus effusus*, *Molinia caerulea* and *L. urens* (Figure 2.18). These quadrats were part of group D, the rough grassland community in Table 2.4.

A further two community types were identified within the park (Table 2.15): quadrats 90 and 91 (group *iv*) were singled out due to their very different community structure. The quadrats were on the banks of one of the parks largest ponds (Figure 2.18), which were heavily disturbed and grazed by birds, so that the community was species poor with only *Raphanus raphanistrum*, *Epilobium montanum* and *L. urens* persisting (Table 2.15). The pH of the soil here, at around 6, was much more alkaline than the rest of the bird park or the surrounding woodland (Figure 2.19). The remaining quadrats, 87, 88, 89, 92 and 95 (group *iii*) were part of grassy woodland edge communities dominated by *Betula pubescens*, *Anthoxanthum odoratum* and *Teucrium scorodonia* (Table 2.15). The environmental variables did not separate groups *ii* and *iii* (Figure 2.19), although the plant communities were obviously different.
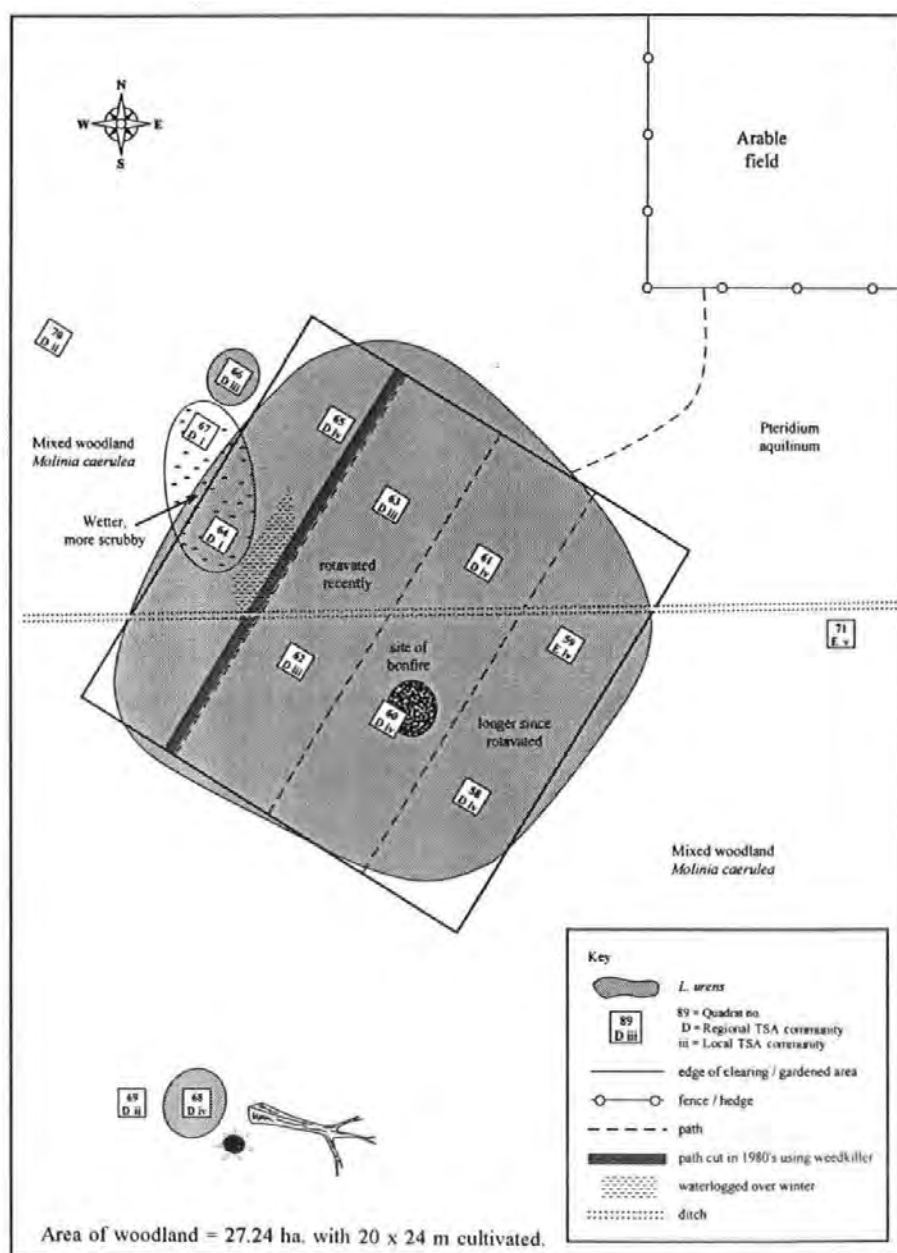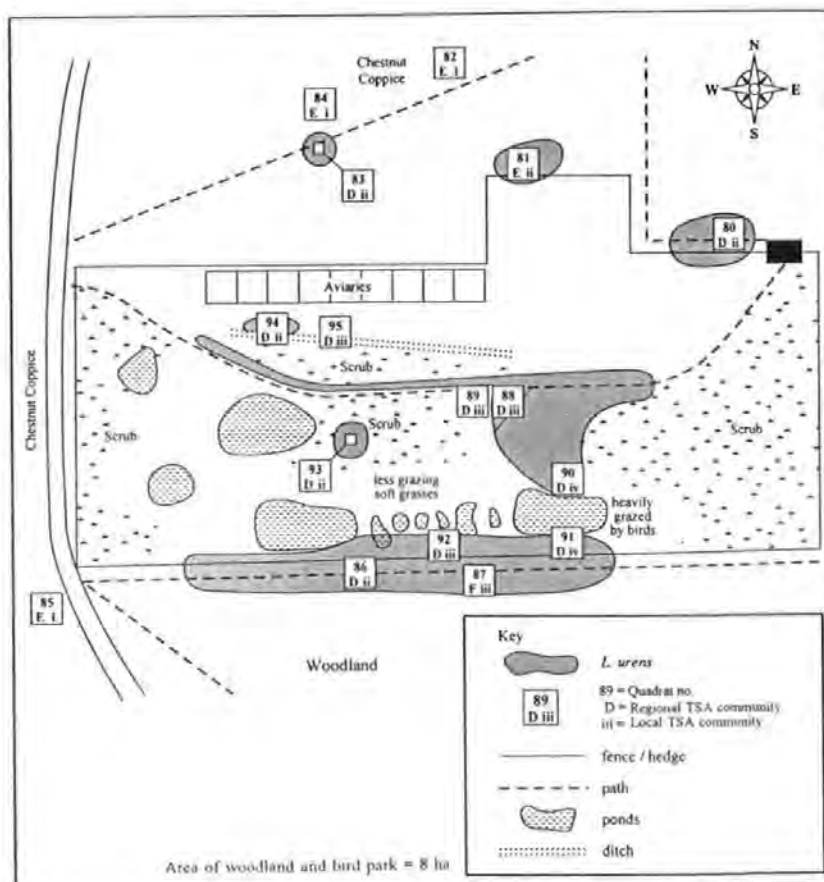

Figure 2.18: Site sketch map with the 16 quadrats of Flimwell, Sussex. The regional and local TWINSPAN (TSA) quadrat groups are indicated.

| | Twinspan group | | | | |
Species	i	ii	iii	iv	Species
Betula pubescens	V 2	VI 2	VI 2		*Betula pubescens*
Pteridium aquilinum	III 2		II 2		*Pteridium aquilinum*
Castanea sativa	VI 3				*Castanea sativa*
Chamerion angustifolium	V 3				*Chamerion angustifolium*
Rhododendron ponticum	V 3	III 3	II 1		*Rhododendron ponticum*
Rubus fruticosus	V 3	III 3			*Rubus fruticosus*
Erica cinerea	III 1	II 2			*Erica cinerea*
Anthoxanthum odoratum		II 2	V 2		*Anthoxanthum odoratum*
Cirsium palustre		II 2	III 3		*Cirsium palustre*
Lotus ulinginosus			II 2		*Lotus ulinginosus*
Senecio vulagris			II 2		*Senecio vulagris*
Teucrium scorodonia			V 2		*Teucrium scorodonia*
Trifolium repens			II 32		*Trifolium repens*
Lysimachia nemorum			III 2		*Lysimachia nemorum*
Ranunculus repens			IV 3		*Ranunculus repens*
Solanum dulamara			II 3		*Solanum dulamara*
Urtica dioica			II 2		*Urtica dioica*
Digitalis purpurea		II 2	II 3		*Digitalis purpurea*
Hypericum humifusum		II 1	II 1		*Hypericum humifusum*
Scutellaria minor		II 2	II 2		*Scutellaria minor*
Cirsium dissectum		III 2	II 2		*Cirsium dissectum*
Juncus effusus		V 3	III 3		*Juncus effusus*
Prunella vulgaris		III 2	II 2		*Prunella vulgaris*
Scirpus supinus		IV 2	III 2		*Scirpus supinus*
Blechnum spicant		III 2			*Blechnum spicant*
Hypericum pulchrum		III 2			*Hypericum pulchrum*
Salix aurita		III 2			*Salix aurita*
Galium palustre		II 1			*Galium palustre*
Holcus lanatus		III 3			*Holcus lanatus*
Molinia caerula	V 2	II 2			*Molinia caerula*
Plantago major	IV 2				*Plantago major*
Potentilla erecta	III 2	II			*Potentilla erecta*
Lobelia urens	V 2	III 2	VI 2		*Lobelia urens*
Centaurium erythraea	VII 2	II 2	IV 2		*Centaurium erythraea*
Epilobium montanum			VI 2		*Epilobium montanum*
Raphanus raphanistrum			VI 3		*Raphanus raphanistrum*

Table 2.15: Species composition of the three community types defined by two-way indicator species analysis of the data from the 16 Flimwell, Sussex quadrats. The first column corresponds to species constancy within each TWINSPAN group (I = 5% or less; II = 6-20%; III = 21-40%, IV = 41-60%; V = 61-80%; VI= 81-100%). The second column indicates average species abundance for each group on the domin scale
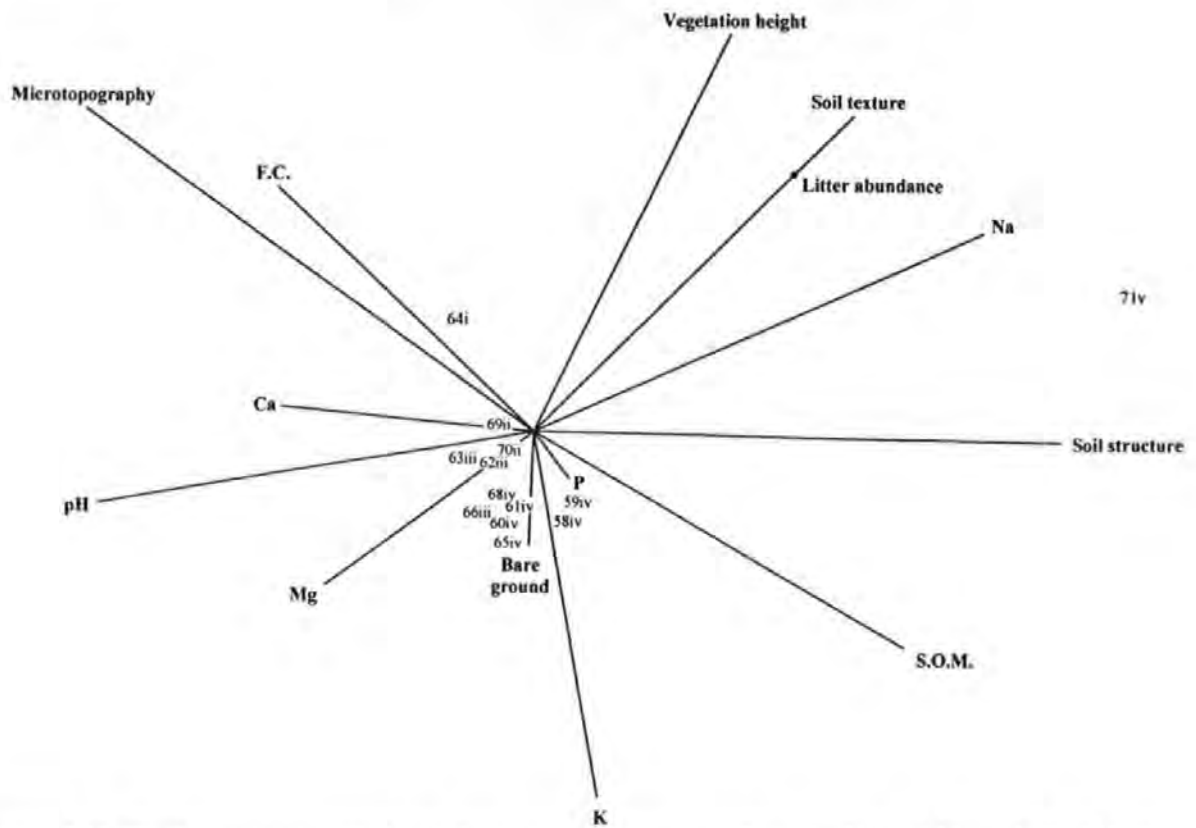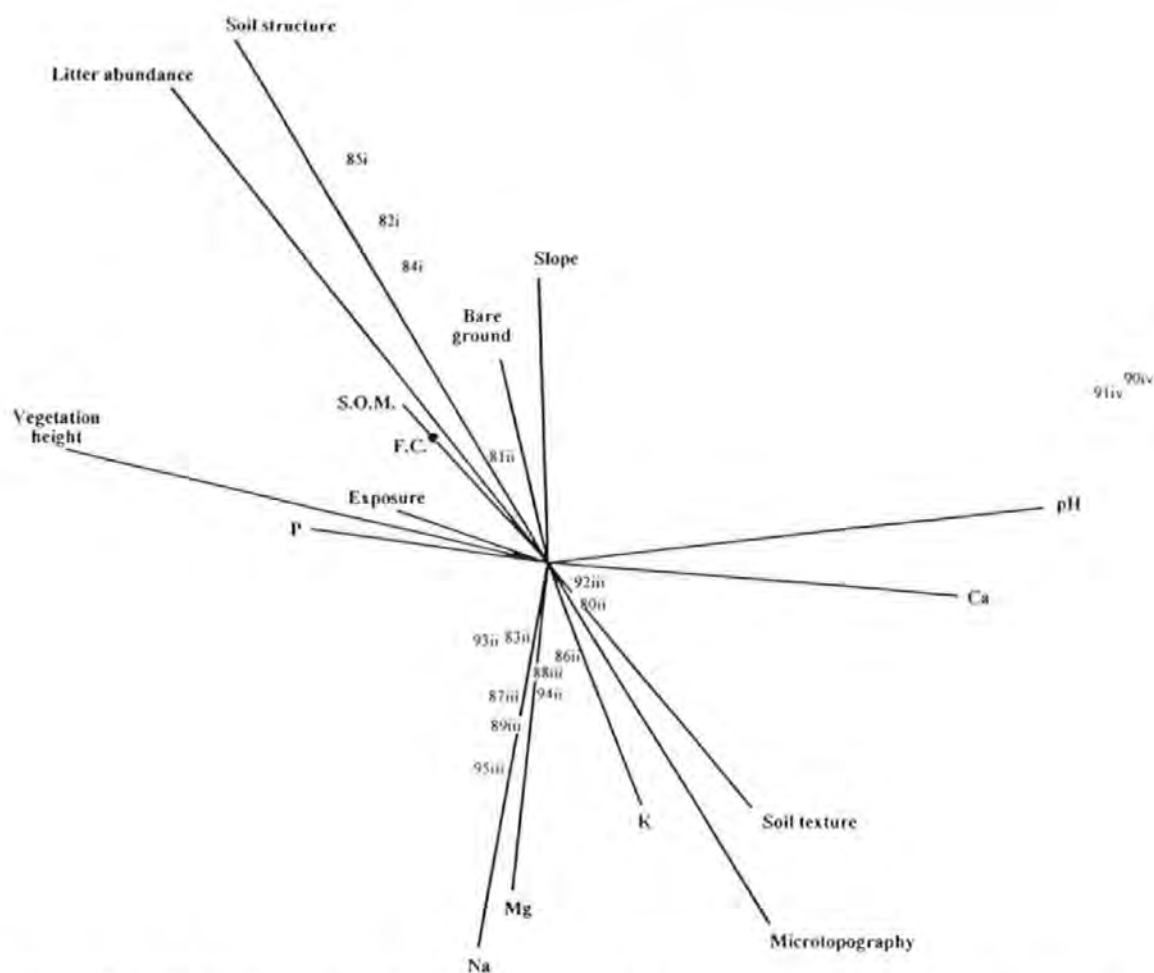
Figure 2.19: Quadrat-environmental biplot from canonical correspondence analysis of the 16 quadrats at Flimwell, Sussex using 15 environmental variables with the distribution of TWINSPAN community groups superimposed (Table 2.15) (Ca, K, Mg, Na and P = soil nutrient status; S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity).

	Slope	Exposure	Vegetation height	Microtopography	Litter abundance	Bare ground	Soil texture	Soil structure	pH	S.O.M	F.C.	P	Ca	Mg	Na
Exposure	-0.20														
Vegetation height	-0.12	0.28													
Microtopography	-0.22	0.29	0.29												
Litter abundance	0.13	0.38	0.40	-0.42											
Bare ground	0.25	0.04	-0.14	-0.33	0.06										
Soil texture	0.02	0.20	-0.09	0.41	0.03	-0.04									
Soil structure	0.38	0.14	0.39	-0.06	0.68	0.09	0.21								
pH	0.33	-0.07	-0.12	0.38	-0.36	0.18	-0.06	-0.09							
S.O.M	0.32	0.01	-0.01	-0.12	0.38	0.16	0.19	0.36	-0.10						
F.C.	0.02	0.05	0.12	-0.17	0.06	-0.23	-0.52	0.07	-0.26	0.01					
P	0.25	0.08	0.47	0.09	-0.02	-0.10	-0.41	-0.15	0.12	0.01	0.26				
Ca	0.41	-0.28	-0.01	0.35	-0.28	-0.10	-0.17	-0.06	0.76	-0.05	0.06	0.28			
Mg	0.39	0.28	0.21	0.51	-0.27	0.18	0.12	-0.02	0.55	-0.11	-0.05	0.32	0.48		
Na	0.17	-0.03	0.33	0.63	-0.37	-0.16	-0.05	-0.10	0.33	0.00	0.16	0.46	0.64	0.70	
K	-0.12	0.55	0.12	0.34	0.06	-0.08	0.08	-0.33	0.07	0.00	-0.07	0.31	0.21	0.24	0.33

Table 2.16: Correlation matrix from canonical correspondence analysis of data from 16 Flimwell, Sussex quadrats using 15 environmental variables (Ca, K, Mg, Na and P = soil nutrient status, S.O.M. = organic matter content of soil; F.C. = soil moisture content at field capacity).

2.6 Discussion

L. urens is in decline in Britain, with ten populations having been lost this century. The remaining *L. urens* sites are environmentally heterogeneous in a number of ways (Figure 2.6). *L. urens* tolerates a full range of soil textures in the surface horizons. The six sites extend from the Curtisen clay of Sussex, through the silty brown-earths of the Yeolland Park association in the West Country, to the well drained Efford 1 sandy loams of Hampshire. Moisture content at field capacity is also highly variable ranging from a mean of 10.6 gcm^{-3} at Kilmington to 34.3 gcm^{-3} at Andrew's Wood (Table 2.3). These variables do not, however, explain the rarity of *L. urens* within southern England. No single environmental factor was solely responsible for the regional abundance of *L. urens* (across all six sites) (Figure 2.8). *L. urens* is less tolerant, however, of variation in pH and soil nutrient status, since all the sites are on moderately acidic pH 4 - 6 (Table 2.3) nutrient-poor, unimproved soils set in low-lying terrain, frequently in valley bottoms. The soils of such areas are often seasonally waterlogged and although the surface horizons at Kilmington, Hurst Heath and Hinton Admiral were predominantly free-draining sandy loams, they are all argillic and lie over more clayey horizons, such as the Barton clay at Hinton Admiral (Findlay *et al.*, 1984; Jarvis *et al.*, 1984). Such undrained, unimproved low-lying land is a rarity itself in southern England and may partly explain the species' scarcity in this part of the country.

Bare ground, percentage litter cover and exposure showed less inter-site variation than the aforementioned variables, and they separated the woodland and grassland communities of each site. Within the fairly specific edaphic requirements, *L. urens* was also found more frequently in the grassland. In southern England, *L. urens* is a member of rough grassland communities, largely M25 - *Molinia caerulea-Potentilla erecta* mire (Tables 2.4 & 2.5), but also occurs in more heathy communities in Hampshire and Dorset. Local analyses of Hurst Heath and Flimwell (Figures 2.14 & 2.18) showed how disturbed open areas within the woodland community, for example those provided by tree fall, supported small numbers of *L. urens* plants. However, without further soil disturbance, *Molinia caerulea* grows very vigorously and the M25

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community generally provides a dense herbaceous cover (Rodwell, 1991b). These grasslands are bordered by mature woodland communities (Figures 2.10, 2.12, 2.14, 2.16 & 2.18 & Tables 2.4, 2.5, 2.7, 2.9, 2.11, 2.13 & 2.15) which, until the middle of this century, were all deciduous (Table 2.1). The grasslands are thus susceptible to scrub invasion from the bordering woodlands, resulting in tall swards (Table 2.3). Mature plants are able to tolerate the dense, high summer swards of the associated plant community (Table 2.3).

Contemporary evidence of the existence of a seed bank which responds to soil disturbance comes from most of the extant sites. Many plants were seen in heavily poached areas at Redlake (Cornwall) and Andrew's Wood (Devon) (Table 2.1) and the population at Flimwell increased dramatically from less than 200 plants to over 2000 after the construction of several ponds, when the site was developed as a bird park (Table 2.1 & Figure 2.18). The number of *L. urens* plants at Hurst Heath rose from 5 to over 150 following the clearance of a narrow strip of land across the heath and numbers are now maintained at around 2000 plants by soil rotovation (Table 2.1 & Figure 2.14). Under the traditional coppice regime at Flimwell, *L. urens* flourished immediately after felling (Table 2.1). At Andrew's Wood 'scalloping' or cutting of the border between woodland and grassland communities to enlarge the transition, resulted in a flush of plants from the seed bank, which grew to an unprecedented size of up to 11 rosettes per plant a year after germination. Similarly, when an acre of woodland was cleared for replanting at Yarner Wood (Devon), *L. urens* reappeared after 40 years of absence. The plants lasted 10 years, probably only a single generation. Again, a fire in the plantation at Hinton Admiral produced a similar short lived population increase (Table 2.1).

Such soil disturbance brings the dormant seeds of the seed bank to the surface and into conditions favourable for germination (Harper, 1977). The decline in *L. urens* would thus appear to be partly due to the absence of soil disturbance following changes in land use and agricultural practice in this century. Firstly, the abandonment of coppicing as a woodland management practice (Rackham, 1986; Peterken, 1993) and secondly the cessation of the use of

rough pasture for grazing horses and cattle with the accompanying exposure of bare soil created by the physical action of trampling during wet months.

This study has shown that *L. urens* is highly threatened in Britain. Restricted to southern England, it is a member of rough, grassy heath communities dominated by *Molinia caerulea* and is situated on seasonally waterlogged, moderately acidic, nutrient poor soils with a history of disturbance events. Conservationists do not necessarily aim to increase the abundance and distribution of naturally rare species (Morse & Lawyer, 1981). However, *L. urens* is not only rare but it is threatened by human activity. Seven of the ten indigenous populations to go extinct this century have been lost through change in land use. At least three of the extant populations (Kilmington, Hurst Heath and Hinton Admiral) are restricted to tiny areas of suitable habitat less than 1000 m^2 (Figures 2.14 & 2.16). There is thus a need to protect and manage *L. urens* in Britain and existing populations will only be maintained and expansion of the present species distribution occur if conservationists devise suitable management plans to improve regeneration. This research suggests high seasonal soil moisture content may be critical for the germination and establishment of *L. urens* and that the species requires sporadic soil disturbance to stimulate emergence from the seed bank. This link between historical ecology, present-day distribution and conservation management would appear very important. The correct foundation and context for the formulation of optimal conservation management plans for rare and threatened species should be laid by a comprehensive biogeographical study as has been presented here.
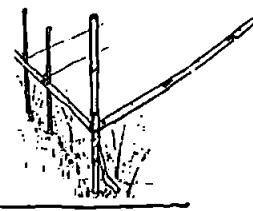
THREE

Demographic monitoring

3.1 Introduction

Although habitat loss is certainly a major cause of modern extinctions (Frankel & Soulé, 1981;

Ehrlich, 1988), demographic and genetic factors make some species especially sensitive to

change in habitat management and environmental perturbations (Frankel & Soulé, 1981; Gilpin

& Soulé, 1986; Lande, 1988). These factors restrict basic demographic processes (Pavlik &

Manning, 1993) such as seed germination (Menges, 1991), seedling establishment (Meredith,

1978; Pavlik & Barbour, 1988), or reproductive output (Griggs & Jain, 1983; Weller & Ornduff,

1991) and thus limit population growth. Such limitations impair the ability of species to recover

from having too few individuals (Pavlik & Manning, 1993) and can then be the cause of rarity

or induce danger of extinction. In order to protect demographically sensitive species, it is

necessary to understand their demography and then to identify the vulnerable stages of their life

cycle and the kinds of perturbations by which they are threatened (Bradshaw & Doody, 1978;

Davy & Jefferies, 1981; Harvey, 1985; Lesica, 1992; Primack, 1993). The key to gaining this

understanding is to monitor repeatedly individuals in the field over time (Davy & Jefferies,

1981; Marcot et al., 1986; Hutchings, 1990; 1991; Primack, 1993). Demographic monitoring is

an essential requirement before sensible decisions can be made as to the best form of

management for the conservation of rare plant populations (Harper, 1977; Menges, 1986;

Hutchings, 1990; Owen & Rosentreter, 1992; Primack, 1993; Given, 1994). Demographic

studies of the rare *Ranunculus ophioglossifolius* provided the basis for a management policy

whose effectiveness has brought the species back from the brink of extinction (Frost, 1981).

Demographically restricted populations often occupy only a fraction of the available habitat,

whereas an optimally managed population would be larger, occupying most of the suitable

habitat, and more likely to contain the diverse genetics and ecological elements necessary for

long-term persistence (Synge, 1981; Schonewald-Cox *et al.*, 1983; Lande & Barrowclough, 1987; Primack, 1993).

This study aimed to investigate the demography of *L. urens* in southwest England. Demographic analyses bring plant ecology within the hard predictive sciences, since they explore the mechanisms that regulate population size (Harper & White, 1974). However, many demographic studies pay little attention to the heterogeneous nature of the habitat, as experienced by the individual plants in populations and therefore the calculated population parameters are often over general and poorly defined (Law, 1981). Here, the populations at two geographically distinct sites, Redlake and Andrew's Wood (Figures 3.1 & 3.2), were monitored to allow both inter- and intra-population variation to be observed. The latter is especially significant at Andrew's Wood, where the disjunct sub-populations occupy separate fields which have quite different management histories and environmental conditions. In addition, light annual grazing was recently reintroduced into the management of Andrew's Wood: herbivory has been found to affect virtually all phases of plant life cycles (Crawley, 1983; 1989). Demographic parameters can ultimately be used to judge management success by comparing the demography of control populations with those of populations subjected to altered management (White & Bratton, 1981; Ehrlén, 1995). However, information on herbivory has only rarely been combined with demographic data in order to assess its effects on the population demography of perennial plants (Crawley, 1989). To observe the effect of grazing on *L. urens*, three exclosures were erected at Andrew's Wood in April 1992, before the cows were let on to the reserve for the first time in ten years.

A group of friend's of Andrew's Wood have conducted an annual census of the *L. urens* flowering population on the reserve since 1972 and a similar census has taken place at Redlake since 1983. Such annual counts of rare species are often the most sophisticated type of data collected for interpreting the efficiency of management. While these data show trends in population size between the two sites and their respective sub-populations over the years, they

long-term persistence (Synge, 1981; Schonewald-Cox *et al.*, 1983; Lande & Barrowclough, 1987; Primack, 1993).

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provide no information on individual performance. Furthermore, the observed net population flux may be merely a damped reflection of reality, due to compensation between individual mortality and recruitment. Counts provide no clues to the way to manage most perennial species (Owen & Rosentreter, 1992) and, in some cases, result in incorrect conclusions about the condition of the population (Hutchings, 1990). As part of this study, annual monitoring of a number of the flowering individuals at Andrew's Wood and Redlake was undertaken for four years using permanent quadrats. Following individual plants from year to year offers the advantage of providing data on growth and longevity, which can then be used to assess the size structure of populations and sub-populations and to determine the relationship between morphology and survival (e.g. Werner, 1975).

An annual census of flowering individuals monitors only one phenological stage of the life cycle of a perennial plant. It can underestimate the true population size and it does not reveal information on the timing of mortality or reflect the rate of turnover in a population. Fortnightly mapping of all individuals within a smaller area of the fifteen permanent quadrats was conducted for twenty-four months at Andrew's Wood and twelve months at Redlake. Frequent close censusing is both rare and valuable (Hutchings, 1990), providing information on phenology, recruitment rates, vegetative growth, flowering and fruiting and on survivorship and the fate of individuals. Together, the two types of census generated the data for the matrix model. Several components of demographic characteristics of long-lived perennials are, however, difficult to establish in the four years of this annual census (Zhang, 1983). The longevity of *L. urens* in the field has not been accurately determined but it is believed to be approximately six to eight years (Brightmore, 1968; Archibald, 1971). At least another four more years of annual census data are required for a complete demographic account of mapped individuals. Long-term demographic studies are still rare, but are crucial to the proper understanding of the population dynamics of species (Crawley, 1990).

3.2 Study sites

3.2.1 *Andrew's Wood, Devon* (Figures 3.1 & 3.3)

Grid Reference: SX 707515.

Conservation status: The site has been a SSSI since 1952 and a LNR since 1965. It has been

owned and managed by the Devon Wildlife Trust since 1972.

Area of reserve: 58.68 ha (4.42 ha under grassland).

Altitude: 140 m.

Situation: On the very edge of moorland in a wide and shallow valley.

Adjacent land-use: Bordered by streams, in an area of arable and improved grassland.

Soil: Silty brown earths of the Yeolland Park Association. Typical Munsell

color - 10YR 6/2 - 5/3. The acidic (pH 4-6), nutrient poor surface

horizons are waterlogged through winter and remain moist (25-48 g

water cm^{-3} soil) in the summer months. They have a variable organic

content (4-30 gcm^{-3}) and a mean bulk density of 0.86 gm^{-3}.

Geology: River gravel and head overlying Meadfoot group (slates with grit) of the

Lower Devonian.

Associated
plant community: Unimproved, wet, acidic grassland. NVC - M25 *Molinia caerulea -*

Potentilla erecta mire, *Angelica sylvestris* sub-community.

Management history: The reserve is a system of old fields with a small area of ancient

woodland. A8 was ploughed in the mid 1960's. The clearings in areas

C and A were grazed and burnt regularly up until 1965 and C was

grazed again over the period 1973-76. Compartment D was grazed

regularly up until 1980. Since they purchased the reserve, The Devon

Wildlife Trust have used annual cutting to abate the scrub. There has

been some drainage in C but there are no records of any artificial

improvement to the nutrient status across the reserve.

Recent grazing :   During the study period, compartments C and D were grazed lightly

between October and December by Guernsey cattle

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Population size: Fluctuating from 100 plants to 5600.

3.2.2 *Redlake Cottage Meadows, Cornwall* (Figures 3.2 & 3.3)

Grid Reference: SX 126592.

Conservation status: Owned by the National Trust, the site has been a LNR managed by the

                        Cornwall Wildlife Trust since 1983.

Area of reserve: 12.50 ha (2.81 ha under grassland).

Altitude: 65 m.

Situation: On low-lying terrain in a shallow valley.

Adjacent land-use: Bordered by streams, in an area of lowland grassland.

Soil: Silty brown earths of the Yeolland Park Association. Typical Munsell

                        color - 10YR 5/3. The acidic (pH 4.5-6), nutrient poor surface horizons

                        which are partly waterlogged through winter and damp (12-28 g water

                        cm^{-3} soil) in the summer months. They have a variable organic content

                        (5-16 gcm^{-3}) with a mean bulk density of 0.53 gm^{-3}.

Geology: Alluvium, head and valley gravel overlying Meadfoot beds (calcareous

                        slates, grit with thin limestone) of the Lower Devonian.

Associated
plant community: Unimproved, damp acidic grassland. M25 *Molinia caerulea - Potentilla*

                        erecta mire, *Angelica sylvestris* sub-community.

Management history: The reserve is a system of old fields which were traditionally used for

                        rough grazing. Several drainage pipes run across the reserve from east

                        to west and into the stream. There are no records of any artificial

                        nutrient improvement across the reserve. The reserve saw no active

                        management between 1963 and 1983 but in 1983 a light grazing regime

                        was adopted by the Trust.

Recent grazing :   During the study period the reserve was grazed from October 1993 to

                        May 1994 by three Exmoor ponies.

Population size: Fluctuating between 10 plants to 1200 but presently on the decline.
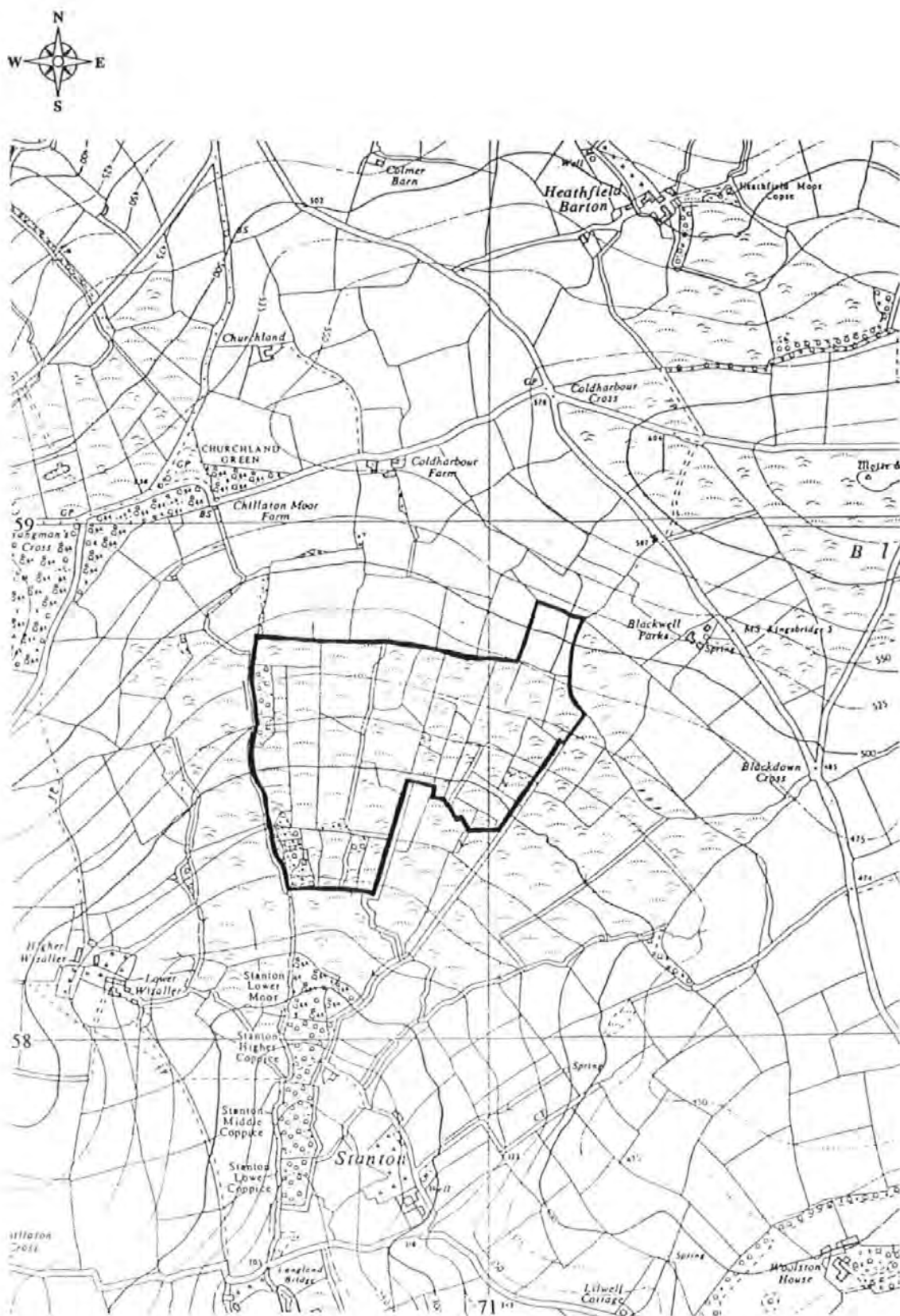
Figure 3.1: The location of Andrew's Wood based on the Ordnance Survey 1:10560 map.
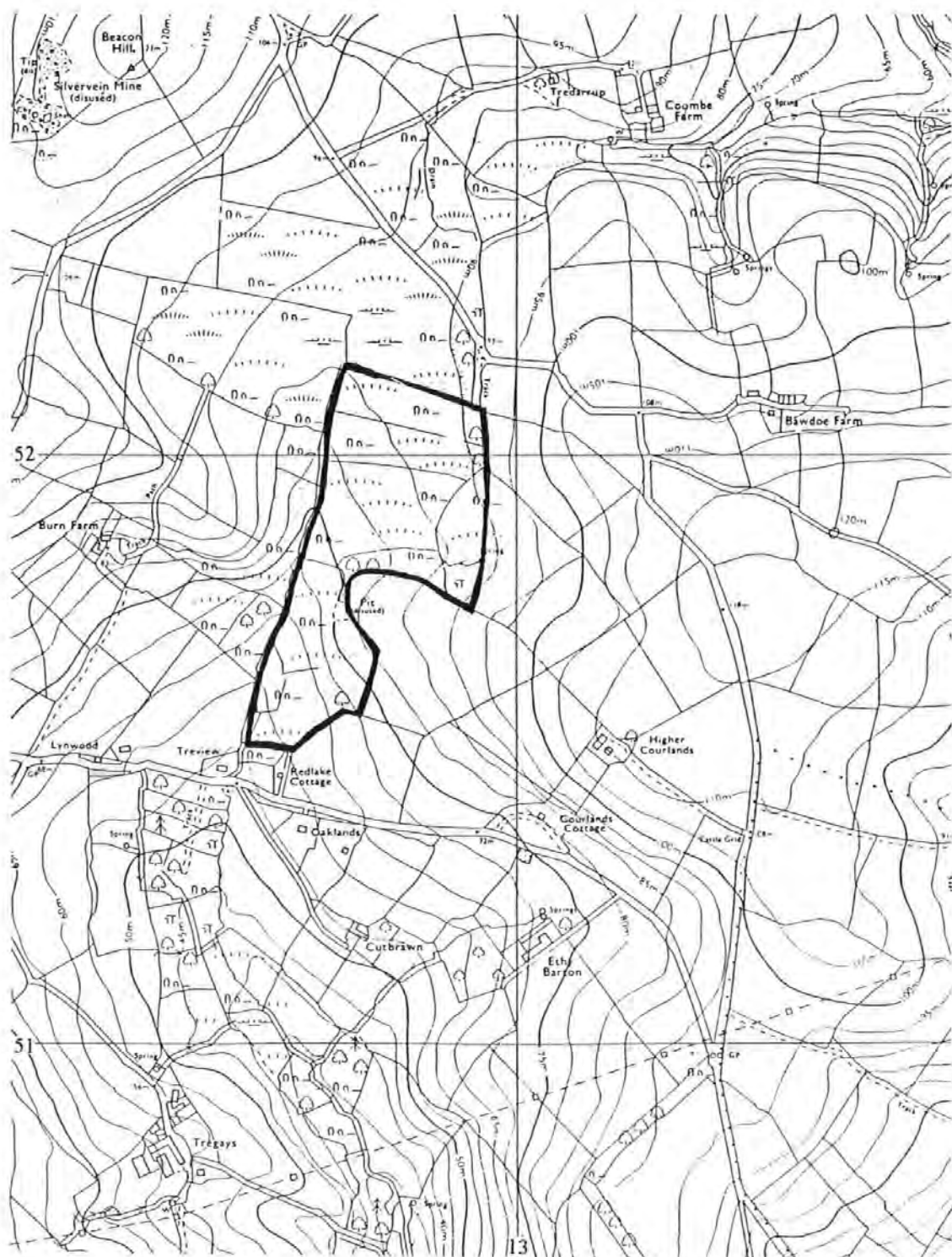
Figure 3.2: The location of Redlake Cottage Meadows based on the Ordnance Survey 1:10560 map.

Andrew's Wood, Devon

Redlake Cottage Meadows, Cornwall
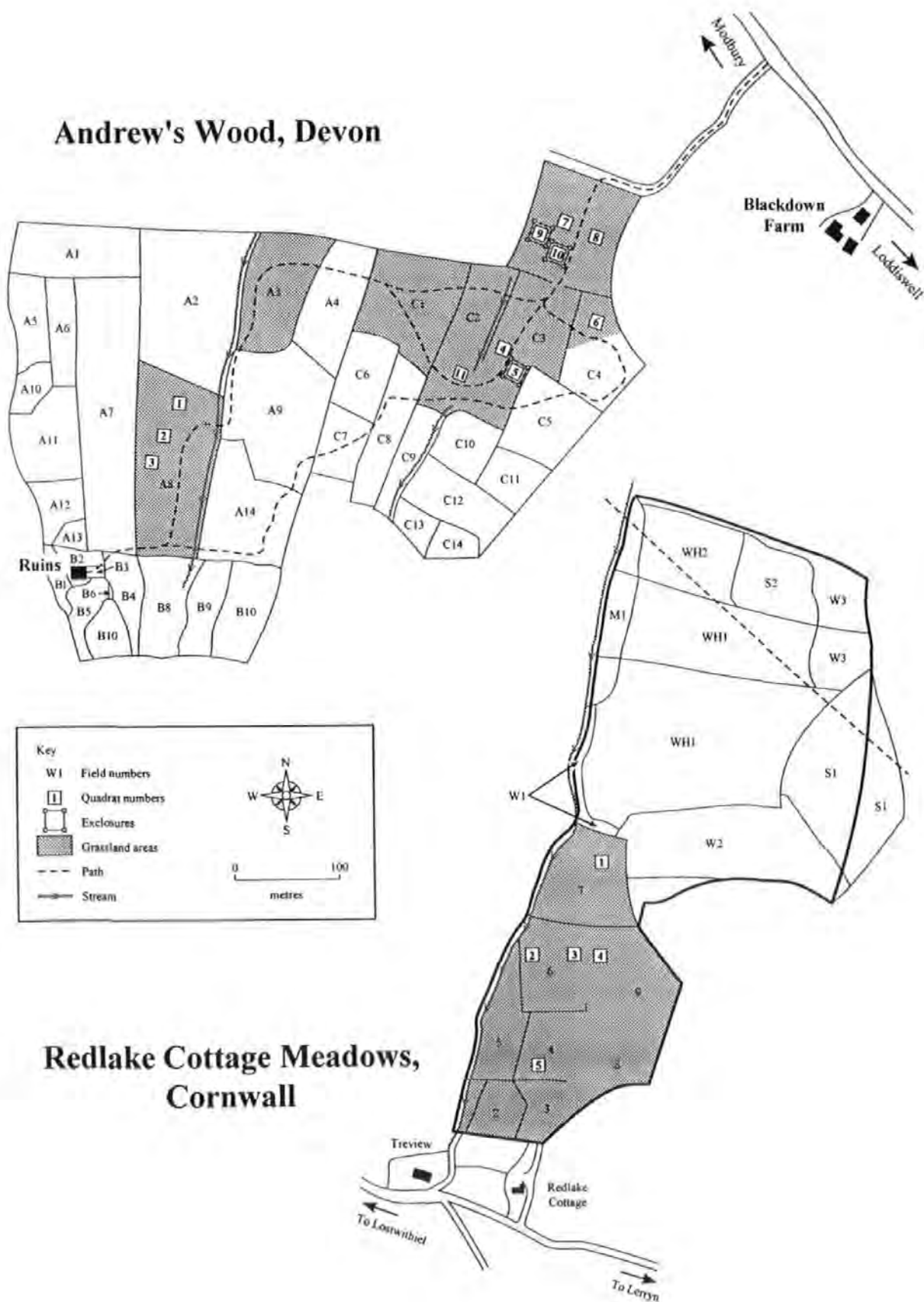
Figure 3.3: Detailed maps of Andrew's Wood and Redlake Cottage Meadows showing individual field numbers and positions of permanent quadrats.

3.3 Methods

3.3.1 *Annual census*

The permanent quadrats measured 5 x 5 m. Five quadrats were erected at Redlake, Cornwall, one in each patch of *L. urens* present in 1992 (Figure 3.3). The larger population at Andrew's Wood was monitored using eleven quadrats. Four quadrats were placed in compartment D, two exclosed controls and two in areas open to grazing. There were four quadrats in compartment C, one control, two grazed and one erected in 1993, after an area of woodland was cleared. There was no access for grazers into compartment A8, where there were three quadrats (Figure 3.3). The quadrats were positioned to encompass the maximum number of plants and marked out with 500 mm lengths of metal piping sunk flush to the ground to ensure against any movement once in place and against any grazing bias that can be induced by posts protruding above ground. Each individual flowering plant occurring within these quadrats was monitored annually for four years beginning in 1992. Recording was carried out in mid-July each year in order to minimized variation arising from phenology and life-cycle (Davy & Jefferies, 1981).

Various methods exist to re-identify plants for repeated censusing, whilst invoking minimal interference with the population directly or indirectly via the immediate environment. The relatively large plot size, the very variable density of the study plants, the high, coarse surrounding vegetation, the extremely wet nature of the soil and proximity to public access were considered carefully when choosing a suitable census technique. The options available and their respective value to this study were as follows (see Hutchings, 1986):

(i) Labelling: Individuals could not be marked using rings since *L. urens* has no permanent aerial structures. Labels which push into the ground would be short-lived, as both sites are waterlogged for much of the year, plus there was the potential for damage from the cattle and ponies.

(ii) Photography: This technique can only be applied unambiguously for either small areas where the vegetation is sparse and essentially single-layered (e.g. Law, 1981) or on a very large scale using aerial photographs (e.g.Pigott & Wilson, 1978).

(iii) Mapping: Sophisticated automated methods of recording population units involve the use of pantographs and mapping tables (e.g. Sarukhán & Harper, 1973; Hawthorn & Cavers, 1976) but these are only accurate when the vegetation is short. Automatic devices such as field digitizers offer great precision, whilst saving time and labour (Mack & Pike, 1979), but regrettably their use is limited due to their expense.

A simple mapping technique was adopted. The permanent quadrats were divided into a grid of 100 smaller squares, each 0.5 m x 0.5 m, using nylon strings held in place by bamboo canes (Figure 3.4a). This grid was reproduced on a recording sheet and the position of each plant was sketched in the corresponding square of the sheet (Figure 3.4b). The number of rosettes and the flowering spike heights were recorded on a separate sheet, using the square coordinates to identify each individual (Figure 3.4c). If more than one plant occupied the same square, then each plant was identified by a letter e.g. 7, 3a and 7, 3b (Figure 3.4).

Some subjectivity was necessary, using knowledge of the behaviour of the plant to determine whether individuals encountered close to the location of a plant the previous year were newly established successors or the previously recorded plant. The rosettes of *L. urens* appear from new rhizome buds each year but the rhizome of *L. urens* is less than 200 mm (Figure 6.6), so it does not make a large contribution to plant movement. Individuals of many species which do not reappear one particular season can still re-emerge in succeeding years (Wells, 1967; 1981; Tamm,1972; Epling & Lewis, 1952). Field observations have shown that *L. urens* is not one such species, and that generally, once it is established, it flowers every year until its death (section 6.3.1). Complications with re-identification were largely due to the very uneven soil surface and obstruction by shrubs. Although in theory, placing the unit dividing tape closer to the ground increases the accuracy, the tussocks of *Molinia caerulea* caused many problems. As a result, accuracy was only to within 15 cm but this was the best possible compromise, considering the size of the plot and rigours of the habitat.

Site:

Quadrat No.:

Date:

Co-ordinates	No. of rosettes	Height of flowering spike (cm)
7,3A	2	71
7,3B	1	58, 62
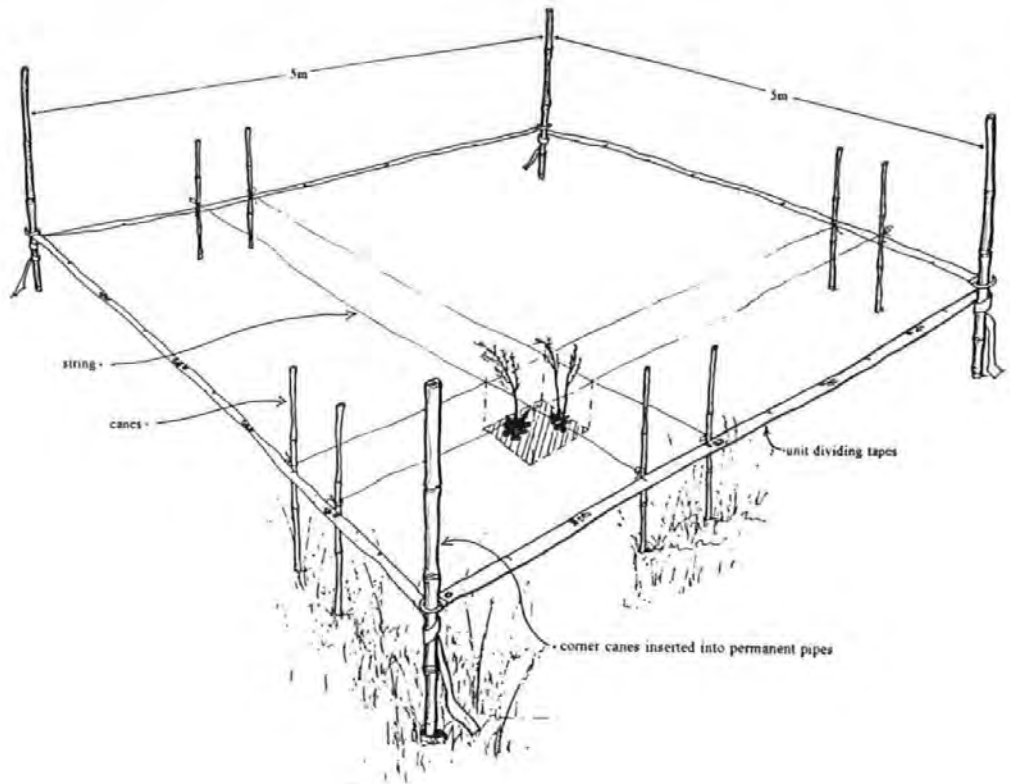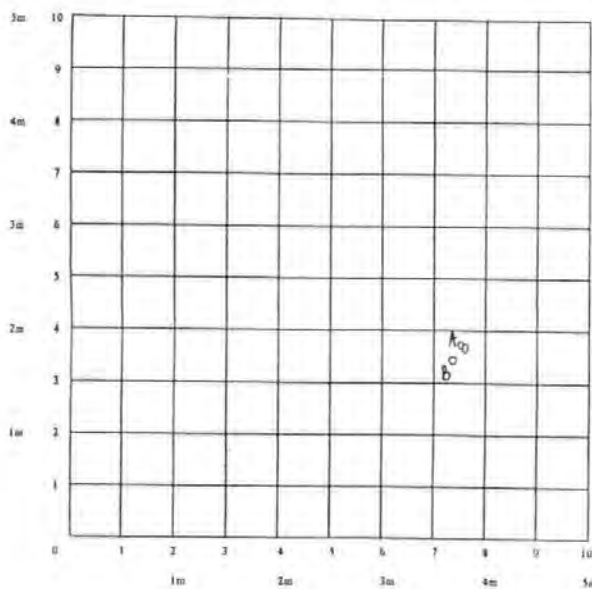
Figure 3.4: The annual census procedure (a) diagrammatic illustration, (b) mapping sheet, (c) data recording sheet.

3.3.2 *Fortnightly census*

Detailed monitoring was performed on all individuals within a single 0.5 m x 5.0 m area adjacent to the edge of each of the original fifteen permanent quadrats (Plate 3.1a). The quadrat erected in compartment C to monitor the recently cleared area of woodland was not monitored fortnightly. To minimise interference of the study area by the researcher, an edge was chosen to enable the observation to be carried out from outside the plot (Plate 3.1b). Second, a smaller area enabled more accurate mapping of individuals due to the decrease in the degree of marginal error. Third, the study area was limited by search efficiency, given the minute size of the seedlings of *L. urens* and the coarse nature of the grassland.

Data were usually recorded at 14 day intervals but recording was less frequent during periods when changes were obviously small (i.e. November to February). Although more frequent visits would have perhaps given a more accurate picture of the flux in the seedling population, a compromise was reached to minimise interference. Over-handling of growing plants is known to increase their respiration (Evans, 1972), the effect is additive and continuous handling results in reduced plant growth (Hutchings, 1986).

The coordinates of each plant present were measured using two unit dividing tapes in parallel, stretching the length of the 5m quadrat, half a metre apart (Plate 3.1a). The distance from the outside edge of the quadrat to the plant was measured using a metre rule at 90° to the tapes. Emergence and mortalities were monitored along with changes in vegetative and flowering morphologies.

Although the habitat imposes the same obstructions on the fortnightly re-identification of individuals as encountered with annual mapping, the smaller area increased mapping accuracy and re-identification was aided by comparisons of individuals leaf length and leaf number. Complications were introduced when grazing and senescence caused a decrease, rather than the expected increase, in size from one census to the next and when trampling, heavy rain, soil invertebrates or other disturbance factors moved seedlings. The accuracy of this smaller scale census was to within 2 cm and was thus much improved over the annual census.

(a)

(b)

Plate 3.1: The fortnightly census procedure (a) the study area of an exclosed quadrat at Andrew's Wood and (b) observations were carried out from outside the plot.

FOUR

Germination

4.1 Introduction

Understanding how environmental factors control population density is a major goal of ecology. Often the dominant factors are not the same across the stages in a species life history. Thus, it is useful to separate the stages. This chapter describes the limitations on the germination of *L. urens*.

A seed is often said to "bet its life" on the favourability of the environmental conditions under which it germinates (from Angevine & Chabot, 1979). Survival chances are improved when the initiation of germination is subject to environmental control (Koller, 1964; Bergleson & Perry, 1989). However, the specificity of the germination requirements is very important; of the enormous amount of seed present in and on the soil, only a small fraction ever germinate (Harper, 1977) and the majority of seeds are thus assumed to never be presented with a suitable environment for germination (Harper *et al.*, 1961). Dormancy, a property which *L. urens* can utilise for long periods in the soil (section 7.3), enhances the resistance of a species to environmental hazards. By prolonging seed survival, dormancy increases the probability of a seed experiencing conditions suitable for germination and establishment.

The ripening, dormancy and germination of seeds is sensitive to a diversity of factors (Angevine & Chabot, 1979), including temperature, moisture, light, gases and minerals. There are numerous reviews of the wealth of laboratory data on the environmental cues involved in the initiation of germination (Heydecker, 1973; Koller, 1972; Mayer & Poljakoff-Mayber, 1982; Harper, 1977; Bewley & Black, 1982). A knowledge of a species germination cues provides an insight into the geographical distribution and habitat preferences of the plant (Thompson &

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Band, 1993).

Temperature cues

The range of temperatures over which a species is capable of germination is a fundamental

determinant the geographical distribution of the plant (Thompson and Band, 1993), since

germination is limited to those climatic regions that have suitable temperatures. Exposure to

diurnally fluctuating temperatures is required to induce many species to germinate (Bewley &

Black, 1982; Thompson & Grime, 1983; Leck, 1989; Thompson, 1993c) and such sensitivity to

varying temperature in the light is thought to synchronize germination of wetland species such

as *Rorippa islandica* and *Gnaphalium uliginosum* with the falling water table in spring

(Thompson, 1993c). Sensitivity to fluctuating temperatures may also function as a depth-

sensing mechanism (Thompson, 1993c) and could partly detect disturbance via the removal of

the insulating effect of vegetation and litter (Miles, 1974; Thompson & Grime, 1983).

Light cues

Light is one of the principal factors controlling dormancy in seeds (Pons, 1992), the response to

which divides seed into four categories, namely, those which germinate:

(i) only in the dark;

(ii) only in continuous white light;

(iii) after being subjected to only a brief illumination and

(iv) those which are indifferent   (Mayer & Poljakoff-Mayber, 1982).

Such a classification is an oversimplification, as seeds are sensitive to not only light intensity

but also light quality. For example, far red light (>700 nm) and light below 290 nm are

inhibitory in their action (Bewley & Black, 1994) and seeds such as *Stachys sylvatica*, which

mature within photosynthetically active capsules, require the stimulus of light to germinate.

Conversely, capsules which senesce earlier (e.g. *Helianthemum chamaecistus*), expose their

ripening seed to unfiltered light, activate seed phytochrome and thus remove the requirement for

light (Cresswell & Grime, 1981). The light requirements of the seed of many species change

with age (Bewley & Black, 1994) and burial often reinstates the seed's requirement for light to induce germination (Wesson & Waring, 1967).

Moisture cues

The germination ability of *L. urens* seed floating in water is of interest, since the sites of extant populations of *L. urens* are all waterlogged to some extent over winter. Seeds must be fixed for establishment (Sagar & Mortimer, 1976) and water affects gas exchange. Specifically, water may reduce the oxygen available to the immersed seed and increase the carbon dioxide (Gulliver & Heydecker, 1973; Meredith, 1978). Both these changes can lower the number of germinating seeds (Mayer & Poljakoff-Mayber, 1982).

Seed dormancy

Innate dormancy (*sensu* Harper, 1957) is common in small-seeded temperate species such as *L. urens* which accumulate persistent seed banks (section 7.3) (Thompson & Booth, 1993) and the germination requirements of such seed is very explicit (Angevine & Chabot, 1979; Probert, 1992). After-ripening or dry storage often reduces the proportion of seeds with innate dormancy and thus the specificity of the germination requirements (Harper, 1967; Thompson & Booth, 1993). In other cases, germination timing is synchronised with a favourable season through a requirement for stratification followed by high temperatures (Meredith, 1978). Dormancy is imposed in some species by the physical restrictions of the seed coat (Sculthorpe, 1967). Such seeds will not imbibe on contact with water and the testa must be breached to induce germination (Leck, 1989).

The interaction between factors

The environmental control of germination is often a complex process involving the interaction of a number of factors. For example:

(i) full light may substitute a requirement for fluctuating temperatures (Tottudel & Roberts, 1980);

(ii) a seed may be light-requiring at one temperature but not at another (Pons, 1992);

(iii) cold stratification may alter the light and temperature requirements (Baskin & Baskin, 1985; Probert *et al.*, 1989; Wulff *et al.*, 1994).

In the field, the temperature, moisture and light environments that are so critical to seed germination are largely controlled by micro-habitat features at the soil surface (Eldridge, Westoby & Holbrook, 1991). Hence, seed germination and establishment are highly responsive to small-scale differences in the soil surface habitat (Harper *et al.*, 1961; Harper *et al.*, 1965; Sheldon, 1974). Regeneration may be affected by physical differences in microtopography (Harper *et al.*, 1965) and by the local abundance of both leaf litter and plants (Goldberg & Werner, 1983; During & van Tooren, 1990; Facelli & Pickett, 1990). Micro-habitats that were found to favour the germination and/or the survival of seedlings have been named "safe-sites" (*sensu* Harper *et al.*, 1961). Since this early work, patterns of emergence and survival have been shown to vary in a complex fashion, not only between species, but also within a species, between years and cohorts (Fowler, 1988; Eldridge *et al.*, 1991).

Laboratory studies of germination responses under controlled conditions are instructive in showing how complex temperature, moisture and light requirements exist and interact. They are not, however, sufficient to predict when and where a seed is capable of germinating and establishing in the field, since the pattern of emergence within a habitat can be achieved by a variety of physiological mechanisms (Angevine & Chabot, 1979). Thus, in this research, the classic laboratory approach was combined with demographic monitoring of emerging individuals to relate laboratory observations to the behaviour of seeds in their natural habitat (Harper, *et al.*, 1965; Harper, 1977; Mayer & Poljakoff-Mayber, 1982; Parone & Reader, 1982).

4.2 Methods

4.2.1 *Controlled laboratory studies*

Seed of *L. urens* was collected in autumn 1993 from arbitrarily chosen points on flowering

spikes of at least fifty individuals from Andrew's Wood. The seed was dried in a desiccator,

then stored in paper at room temperature for at least nine months: seeds are generally fully

ripened after three months (Thompson & Booth, 1993). The seeds of *L. urens* were not stored

in the dark, since they are exposed to unfiltered sunlight through the capsule whilst ripening on

the plant.

The range of constant temperatures over which *L. urens* is capable of germination was

investigated on a thermogradient bar between 5-35°C at the Unit of Comparative Plant Ecology,

Sheffield. Seeds were kept moist throughout and light was provided for 13 hours per day by

incandescent strip lights at an intensity of 6 μmol m^{-2} sec^{-1}. The germinating seedlings were

counted daily, using protrusion of the radicle as the criterion for germination and the final

germination percentages were determined after twenty-five days incubation. The results of the

thermogradient bar tests indicated that the optimum constant temperature for germination was

29°C (Figure 4.1).

Since germination is usually more enhanced by alternations at sub- rather than supra-optimal

temperatures (Thompson, 1993c), the response to alternating temperatures was than tested at

13°C:6°C, 20°C:9°C, and 29°C:15°C (14:10 hrs synchronised with photoperiod). These

temperatures approximate to the mean daily maximum and minimum temperatures in southern

England in spring (13:6°C) and summer (20:9°C) (unpublished Plymouth meteorological office

data 1970-1995) and an alternation which is of similar amplitude and uses the optimum constant

temperature (Figure 4.1) as the daytime (29:15°C). This highest temperature is comparable to

summer-time in north-central Spain (Pearce & Smith, 1984), the centre of the range of *L. urens*.
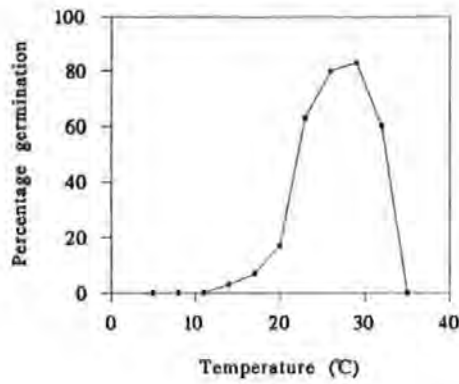
Figure 4.1: Total germination of *L. urens* seed over a range of constant temperatures (Unit of Comparative Plant Ecology, Sheffield).

A single lot of 100 seeds was sown under each treatment; each lot on a cotton wool pad covered with a Whatman No. 1 filter paper in a 60 mm glass petri-dish, the pad standing in 2-3 mm of water throughout. The petri-dishes were used upside down with the smaller half, which is conventionally the base, functioning as the lid so that the water condensing on the upper surface was directed back into the dish. Together, these two measures ensured that, although not standing in water, the seeds were never allowed to dry out. Germination tests were performed in a Sanyo MIR - 152 incubator. Light was provided for 14 hours per day by (cool white) fluorescent light at an intensity of ca. 20 μmol m^{-2} sec^{-1} (400-700 nm) referred to as 14:10 hrs from now on. The dishes were checked for water and the germinating seedlings counted daily. The final germination percentages were determined after 30 days of incubation.

Within the three alternating temperature treatments, a further two parameters were investigated:

(i) comparison of the germination of flooded seed with those kept moist. Seed was sown into petri-dishes without cotton or filter paper. A circle of stiff nylon gauze (0.25 mm gauge) was inserted above the seed. The dish was fully immersed in water and the lid (smaller half) was lowered to rest on the gauze; care was taken to ensure no air was trapped in the lid. The dish was then taken out of the water and placed in the incubator. The gauze prevented the seed from escaping whilst the dish was submerged but still allowed them to float (Figure 4.2).

petri-dish

water

gauze

seeds
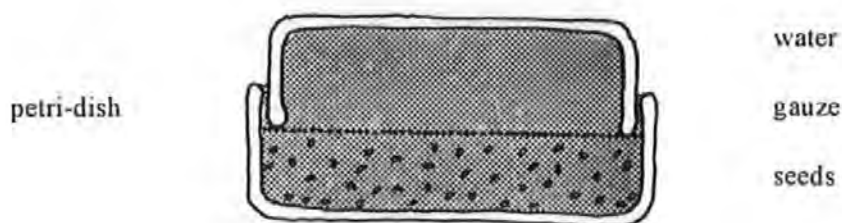
Figure 4.2: The method of submerging seed in water.

(ii) observation of the effect of full darkness on germination. Dishes were covered in a double layer of aluminium foil. For a 30 day incubation period, 10 dishes were set up and every third day, a dish was uncovered to count germinating seeds. Once exposed to light, the dishes were discarded.

The requirement of *L. urens* seed for after-ripening and stratification was investigated at a single alternating temperature treatment, 20°C:9°C (14:10 hrs). This combination was chosen, since it approximates the average temperatures that seed would be subjected to on ripening in southwest England in August-September (unpublished Plymouth meteorological office data 1970-1995).

(i) investigation of the need for after-ripening. 200 early-ripening seeds were collected on August 1 1995 at Andrew's Wood. The seed was dried in a desiccator for 24 hours and incubated as described above, with 100 in darkness and 100 under a fixed photoperiod at 20°C:9°C (14:10 hrs). The final germination percentages were determined after 21 days of incubation.

(ii) assessment of the need for stratification. Two hundred seeds were spread on cotton pads, constantly soaked in 2-3 mm of water, covered in Whatman No. 1 filter paper and kept in the refrigerator at 4-5°C. Chilling is effective in light or darkness (Thompson & Booth, 1993), hence seeds were not shaded from the light. The maximum period required for the stratification

of the vast majority of species is 13 weeks (Thompson & Booth, 1993). Thus, after 13 weeks of this pretreatment, the seeds were incubated (100 in darkness, 100 under a fixed photoperiod) under the 20°C:9°C (14:10 hrs) regime. The final germination percentages were determined after 21 days of incubation.

4.2.2 *Field demography*

The emergence of seedlings was recorded as part of the fortnightly census described in section 3.3.2 and this included a record of the nature of the soil surface beneath the new recruits. Quantification of the soil surface micro-habitat is very difficult, especially at small scales (Sanson, Stolk & Dornes, 1995) and consequently the four chosen factors, ground cover by higher plants, litter, moss and soil surface depressions, were categorised on their presence or absence. In addition, in 1994 the interference from higher plants was quantified at both sites as the proximity to the nearest neighbouring adult plant of the same or of a different species, referred to as the nearest neighbour distance (NND). The frequency of the soil surface micro-habitats and the distance to nearest neighbours in each quadrat was recorded using 100 randomly positioned pins per census quadrat at Redlake and Andrew's Wood in July 1994 and again in July 1995.

4.2.3 *Experimental seed bed*

An experimental seed bed was used to investigate further the effect of the different micro-habitats on germination and survival. The bed consisted of a wooden box 900 mm x 1200 mm and 200 mm deep, housed in an unheated glasshouse, filled with John Innes No. 2 compost and watered from below using capillary matting fed from a reservoir (Plate 4.1a). The effects of four soil surface factors were investigated: shade, litter, moss and depressions. Shade was provided by a double layer of green nylon glasshouse shading mesh, which reduced light intensity in full sun from 1032 μmol m^{-2} sec^{-1} to 26 μmol m^{-2} sec^{-1} (i.e. 25% full daylight).

The bryophyte species used to create the moss layer were *Pseudoscleropodium purum* and *Rhytidiadelphus squarrosus*, two species found commonly in Andrew's Wood and the litter was that of *Molinia caerulea*, the most abundant litter producer at both Andrew's Wood and Redlake. To simulate the effect of poaching on soil surface topography and compaction, a plant pot was pushed into the compost creating a depression 50 mm in both diameter and depth.

Dividing the bed into two blocks of 24 150 mm^2 plots allowed an analysis of the difference in soil moisture between the ends closest to and furthest away from the reservoir. Within the two blocks a nested design permitted the analysis of all the possible interactions between the four soil surface factors. The design was such that the greatest number of degrees of freedom were attributed to the most important factors, as suggested by field observations (Table 4.1). In each of the 48 plots, shade, moss and litter were either present or absent (Plate 4.1b). There were three levels of soil surface topography: flat and with one or two depressions. This allowed an analysis of the effect of both a depression and of the raised area created between two depressions.

Seed was collected and stored as described previously (section 4.2.1). Before germinating seed for an experiment, it is necessary to be aware of its viability (Booth & Hendry, 1993). Since the experiment was to be run in the glasshouse at ambient temperatures from mid-May to mid-July, viability of the seed at these seasonal temperatures wasu tested by running five replicates of 100 seeds each, in petri-dishes containing two filter papers kept damp with deionised water. The dishes were checked for water and germinated seed counted daily. After 30 days, germination was 20%. Using this germination rate, to obtain a density of seedlings sufficient to detect variation with micro-habitat, without invoking density dependent stress (estimated to be 40 seedlings per 150 mm^2 plot) required a total of 9600 seeds for the 900 mm x 1200 mm seed bed. As the average weight of a seed was 18.3 µm , 175.7 mg of seed was required. The seed was mixed with sand of similar dimensions and then divided into four equal portions. One quarter was scattered from each edge of the bed to give an even density over the plots.

(a)

Seed bed

Capillary matting

Water reservoir

(b)

Plate 4.1: Seed bed experiment (a) set-up and (b) 48 individual plots with combinations of the four soil surface factors.

	d.f.	residual d.f.		d.f.	residual d.f.
S	1		M	1	
B	1		M x S	1	
S x B	1	2	M x D	2	
			M x S x D	2	
D	2		M x L	1	
D x S	2		M x S x L	1	
D x B	2		M x S x L x D	2	
D x S x B	2	4	M x B	1	
			M x S x B	1	
L	1		M x D x B	2	
L x S	1		M x L x B	1	
L x D	2		M x S x D x B	2	
L x S x D	2		M x S x L x B	1	
L x B	1		M x D x L x B	2	
L x S x B	1		M x S x D x L x B	2	12
L x D x B	2				
L x S x D x B	2	6			

Table 4.1: Allocation of degrees of freedom (d.f.) to each of the four soil surface types used in the seed bed (S = shade, M = moss, L = litter, D = depressions and B = block).

Seed was sown on May 21 1994 and germination began on June 6. Emergence was mapped and survival followed every other day for the duration. Germination tailed off after 63 days and the experiment terminated on July 23 1994.

4.3 Results

4.3.1 *Controlled laboratory studies*

L. urens is capable of germinating between the constant temperatures of 14°C and 32°C (Figure 4.1). The optimum constant temperature for the species is 29°C (Figure 4.1).

Between the constant temperatures of 23°C and 32°C, germination commenced after four days incubation and was largely complete after ten days. The germination rate was much slower at temperatures lower than 23°C (Figure 4.3).
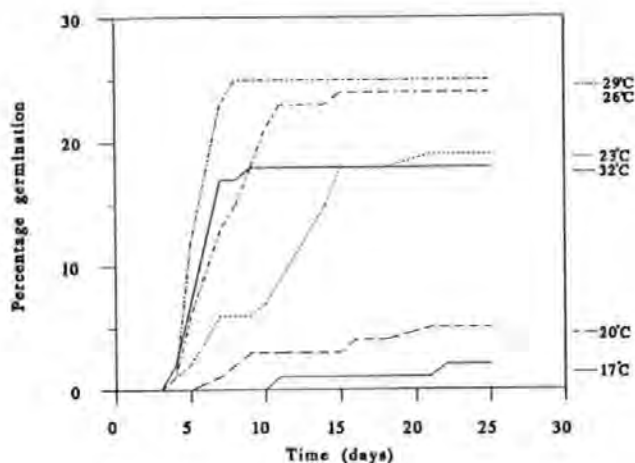
Figure 4.3: Germination rate of *L. urens* seed over a range of constant temperatures.

Germination at sub-optimal alternating temperatures did not produce any increase in percentage germination or rate compared to constant temperatures (Figure 4.4). An increase in percentage germination was seen with an increase in temperature over the three alternating temperatures investigated (Figures 4.4, 4.5 & 4.6).
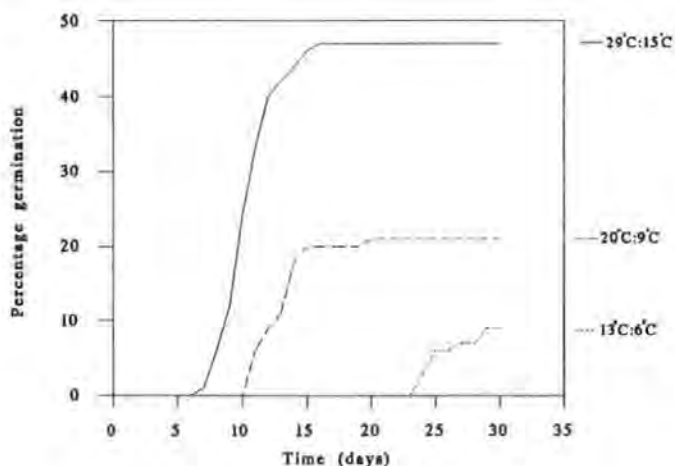
Figure 4.4: Germination rates of *L. urens* seeds kept moist at three alternating temperatures (14:10 hr thermo- and photoperiod).

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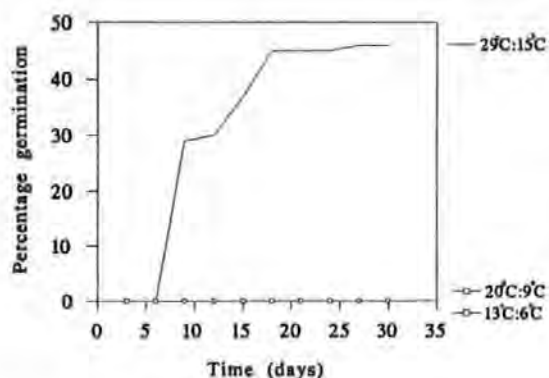
Figure 4.5: Germination rates of seeds kept moist and under constant darkness at three alternating temperatures (14:10 hr thermoperiod).
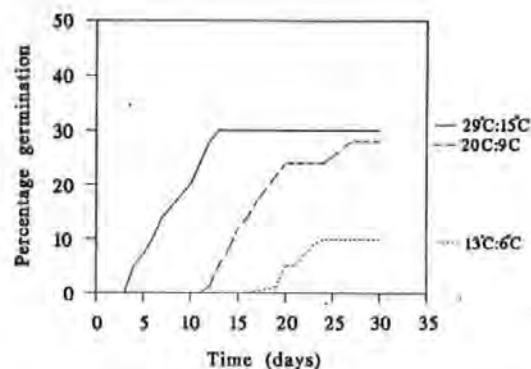
Figure 4.6: Germination rates of seeds flooded at three alternating temperatures (14:10 hr thermo- and photoperiods).

L. urens is light-requiring at 13:6°C and 20:9°C but percentage germination in darkness at 29:15°C was at a similar level to that in the light (Figures 4.4 & 4.5). Seed can germinate when floating in the water column in the light (Figure 4.6) and at 13:6°C and 20:9°C, percentage germination is similar between flooded and moist treatments (Figure 4.4 &4.6). At 29:15°C, flooded seeds have a higher percentage germination than at 20:9°C but show a reduced success compared to their moist counterparts (Figure 4.4 & 4.6).

L. urens seeds began to swell two to four days after moistening. There was therefore no requirement for scarification. The percentage germination of fresh seed was not different from seed which had been in dry storage for two years. Thus, there was no requirement for after-ripening (Figure 4.7). Stratification did not affect percentage germination in darkness, which was still inhibited, but it did induce a considerable improvement in germination under the photoperiod (Figure 4.7).

4.3.2 *Field demography*

Emergence peaked at Andrew's Wood in June both in 1993 and 1994 (Figure 4.8). Fortnightly censusing was only undertaken at Redlake in 1994 (section 3.3.2). In 1994, emergence at Redlake was restricted to the months of June and July, which coincided directly with the
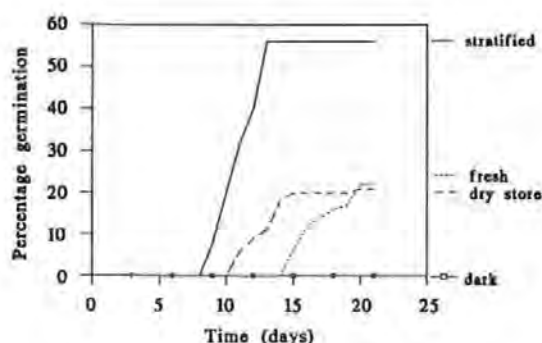
Figure 4.7: Germination rates of seeds under 20:9°C (14:10 hr thermo- and photo periods) with different pretreatments (Dark = stratified, dry stored and fresh seeds incubated in darkness).

removal of the ponies in May 1994 (section 3.2.2). Within Andrew's Wood, the grazed areas of compartments C and D (Figure 3.3) both had moderate levels of recruitment (mean ≈2 seedlings m^{-2} month^{-1}) across 1993 and 1994 (Figure 4.8). In June and July 1994, emergence in compartments C and D was comparable to Redlake (Figure 4.8). In contrast, the equivalent quadrats within the ungrazed exclosure of these same compartments recruited virtually no new plants. No new seedlings emerged from ungrazed C and only four seedlings, over the 20 month census, were found in the ungrazed D (Figure 4.8).

Compartment A8 showed similar emergence to the grazed quadrats of compartments C and D in 1993. However, in 1994, emergence in A8 soared (Figure 4.8). There were no changes in the management of A8 during 1992-1994 which could explain this increased emergence. Figure 4.9 shows that summer 1994 was warmer than that of the previous year. The major difference between A8 and compartments C/D is that A8 is not grazed but still maintains a more open sward (Figure 4.10) through which a higher ratio of red to far-red light passes to ground level (Table 4.8) and, higher ground temperatures may be reached. A8 is less exposed and also slightly drier than C and D (Table 4.2).
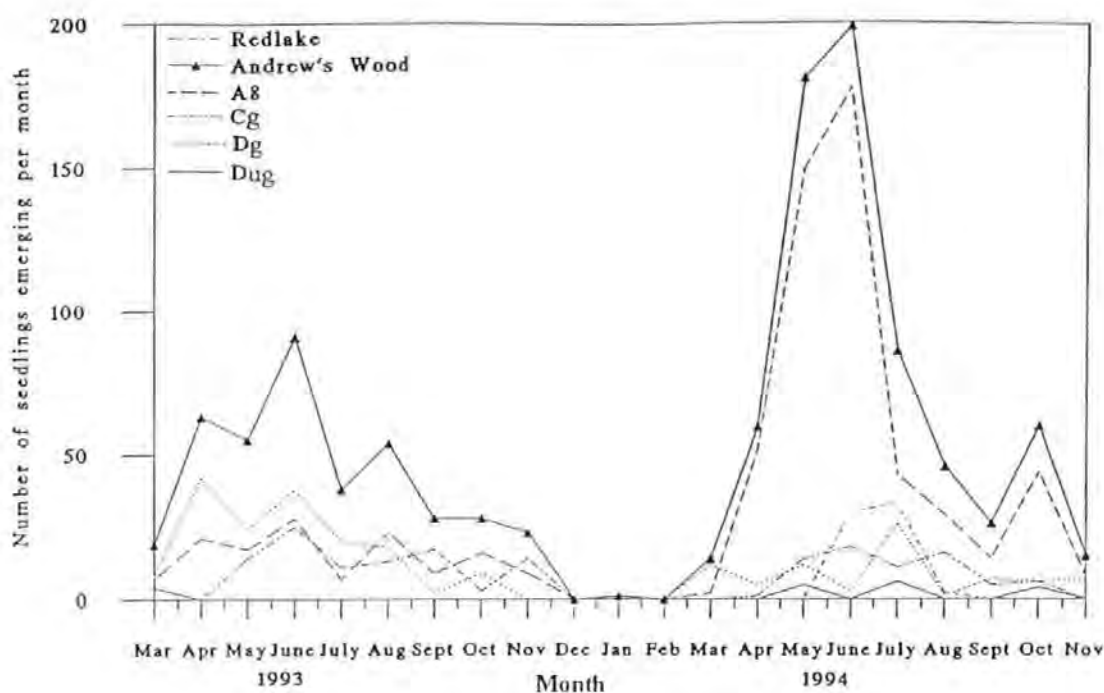
Figure 4.8: Timing of emergence in 1993 and 1994 at Redlake and Andrew's Wood and within Andrew's Wood in compartments A8, the grazed areas of C (Cg) and D (Dg) and the ungrazed exclosure within D (Dug). The number of seedlings in the compartments of Andrew's Wood are expressed per 5 m². The number of seedlings for the two sites, Andrew's Wood and Redlake, are expresses per 20 m².
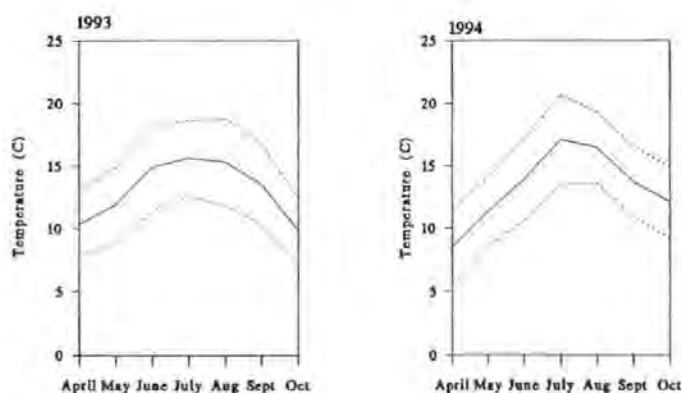
Figure 4.9: Comparison of mean daytime maximum, night-time minimum and twenty-four temperature in Plymouth, April to October 1993 and 1994.

Small numbers of seeds germinate throughout March to November but the total emergence at Andrew's Wood has a main pulse which commences as temperatures rise in May and continues through to June. Although temperatures remain high through July and August, emergence tails off until a second cohort emerges later on, in August in 1993 and October in 1994. Compartment A8 is largely responsible for this two cohort phenomenon.

Environmental variable	Compartment		
	D	C	A8
R:FR	0.62	0.69	0.74
Vegetation height (cm)	36	32	25
Slope	5.6	5.0	3.5
Bare ground	3.1	3.5	3.2
Bryophyte cover	1.3	1.6	2.1
Litter abundance	2	2.4	4.2
Micro-topography	3.3	3.1	2.4
Exposure	4	4	5
Soil texture	4	4	4
Soil structure	2	2	2
Soil pH	5.5	5.0	4.78
Organic matter content (% mg cm^{-3})	20.6	11.2	11.9
Drainage	3.6	2.8	2.4
Moisture content (% mg cm^{-3})	40.3	33.8	30.2

Table 4.2: Mean environmental values for compartments C, D and A8 of Andrew's Wood (for explanation of scales see section 2.3.3)

The micro-habitat frequency census at Andrew's Wood recorded no occurrences of the presence of higher plants (G) in conjunction with soil surface depressions (D): comparison of data for 1994 and 1995 showed little difference between the two years (Table 4.3). In contrast, there was a shift in micro-habitat availability at Redlake. Micro-habitats with all four factors present were less frequent, as was the presence of ground cover by higher plants with litter, whilst only ground cover by higher plants, and moss or only depressions were more common (Table 4.3).

The counts of the number of seedlings emerging under each micro-habitat type at Andrew's Wood in 1993 and 1994 and at Redlake in 1994 were used in conjunction with the data on micro-habitat frequency for 1994-5 (Table 4.3) in the following formula to give the relative emergence for each micro-habitat type:

Relative emergence =

$$\frac{\text{micro-habitat emergence count}}{\text{micro-habitat frequency} \times \text{total emergence}}$$

Favourable micro-habitats have scores greater than one and those which are unfavourable less than one.

micro-habitat				Frequency			
				Andrew's Wood		Redlake	
G	M	L	D	1994	1995	1994	1995
1	1	1	1	0	0	0.033	0.013
1	1	1	0	0.020	0.016	0.073	0.047
1	1	0	1	0	0	0	0
1	1	0	0	0.008	0	0.007	0.100
1	0	1	1	0	0	0.127	0
1	0	1	0	0.448	0.508	0.133	0.107
1	0	0	1	0	0	0	0
1	0	0	0	0.152	0.130	0.127	0.153
0	1	1	1	0.012	0.008	0.033	0.033
0	1	1	0	0.088	0.076	0.053	0.067
0	1	0	1	0.006	0.010	0.047	0.053
0	1	0	0	0.026	0.024	0.013	0.027
0	0	1	1	0.070	0.076	0.100	0.113
0	0	1	0	0.138	0.120	0.107	0.140
0	0	0	1	0.002	0	0.033	0.053
0	0	0	0	0.030	0.032	0.120	0.093

Table 4.3: Random point frequency of soil surface micro-habitats produced from the presence (1) or absence (0) of all combinations of four surface types (G = ground cover by higher plants, M = moss, L = litter, D = depressions) at Andrew's Wood (AW) & Redlake (RL) 1994-1995.

No statistical analyses could be applied to these relative emergence figures, since emergence was too frequently zero to use a multifactor ANOVA. Chi-square tests for association, G-tests and log-linear models can only be carried out using frequency counts. When used alone, counts of the number of seedlings emerging under each micro-habitat were of little value, as they did not take into consideration the micro-habitats frequency and hence a high count may have indicated the favourability or prevalence of a habitat. The results expressed as relative emergence (Table 4.4) were considered important, especially when consistent over two years of census and across both sites, and were sufficiently straightforward to be of use.

micro-habitat				Relative emergence			micro-habitat rating
G	M	L	D	AW93	AW94	RL94	
1	1	1	1	0.000	0.000	0.000	x
1	1	1	0	0.510	2.504	0.926	~
1	1	0	1	0.000	0.000	0.000	-
1	1	0	0	3.508	1.836	0.463	~
1	0	1	1	0.000	0.000	0.000	x
1	0	1	0	0.030	0.059	0.000	x
1	0	0	1	0.000	0.000	0.000	-
1	0	0	0	0.000	0.167	0.000	x
0	1	1	1	13.818	2.671	0.617	~
0	1	1	0	4.435	4.048	3.333	✓
0	1	0	1	6.803	1.836	1.111	✓
0	1	0	0	8.144	2.727	8.769	✓
0	0	1	1	0.182	0.238	0.412	x
0	0	1	0	0.444	2.170	0.337	~
0	0	0	1	7.653	2.671	0.617	~
0	0	0	0	1.700	4.090	0.265	~

Table 4.4: Relative emergence under differing soil surface micro-habitats produced from the presence (1) or absence (0) of all combinations of four surface types (G = ground cover by higher plants, M = moss, L = litter, D = depressions) at Andrew's Wood (AW) & Redlake (RL) 1993-1994. Micro-habitat rating key (-) absent, (~) inconsistent with respect to emergence, (✓) favourable to emergence (relative emergence always ≥ 1) and (x) unfavourable to emergence (relative emergence always < 1) .

Three of the five unfavourable micro-habitats featured litter without moss. All three favourable micro-habitats featured the presence of moss without ground cover by higher plants. There were six habitats with inconsistent emergence results: four of these were favourable to emergence at Andrew's Wood but not at Redlake. Only 54 seedlings emerged at Redlake during the single census year of 1994 compared to 1087 at Andrew's Wood over the two years census 1993-1994. Therefore the Redlake results were of less value. The presence of litter and ground cover strongly inhibited the germination of *L. urens* seedlings whilst moss was facilitative. The effects of topography were not clear from these results (Table 4.4).

The field observations of the frequency of distances to each emergent seedling's nearest

neighbouring adult (NND) were not significantly different between 1994 and 1995 (two sample comparison, Mann-Whitney U, test statistic, Z = - 0.49). Compartment D had the highest occurrence of NND = 0cm, i.e. the tightest sward, with ungrazed quadrats being slightly tighter than the grazed (Figure 4.10e & f). Redlake and Compartment A8 has the least occurrences of NND = 0 cm and proportionately more NNDs greater than 4 cm, i.e. the most open sward (Figure 4.10b & g).

Table 4.5 shows chi-square test for association between distance to nearest neighbour (NND) and the observed number of seedlings emerging at Redlake and Andrew's Wood and for each of the compartments within Andrew's Wood. Data from the survey of the NND to random points (Figure 4.10) were used to calculate the expected values (relative abundance of each NND in that reserve/compartment x total number of emergent seedlings in that reserve/compartment).

(a)

NND (cm)	0	1	2	3	4	5	6	7	8	9+
Observed	85	24	76	84	68	72	45	16	30	133
Expected	400	9	38	53	39	32	18	11	13	23

Andrew's Wood, 1994 χ^2 =991, d.f. = 9, $P < 0.001$.

(b)

NND (cm)	0	1-3	4+
Observed	8	48	0
Expected	25	14	5

Redlake, 1994. χ^2 =109, d.f. = 2, $P < 0.001$.
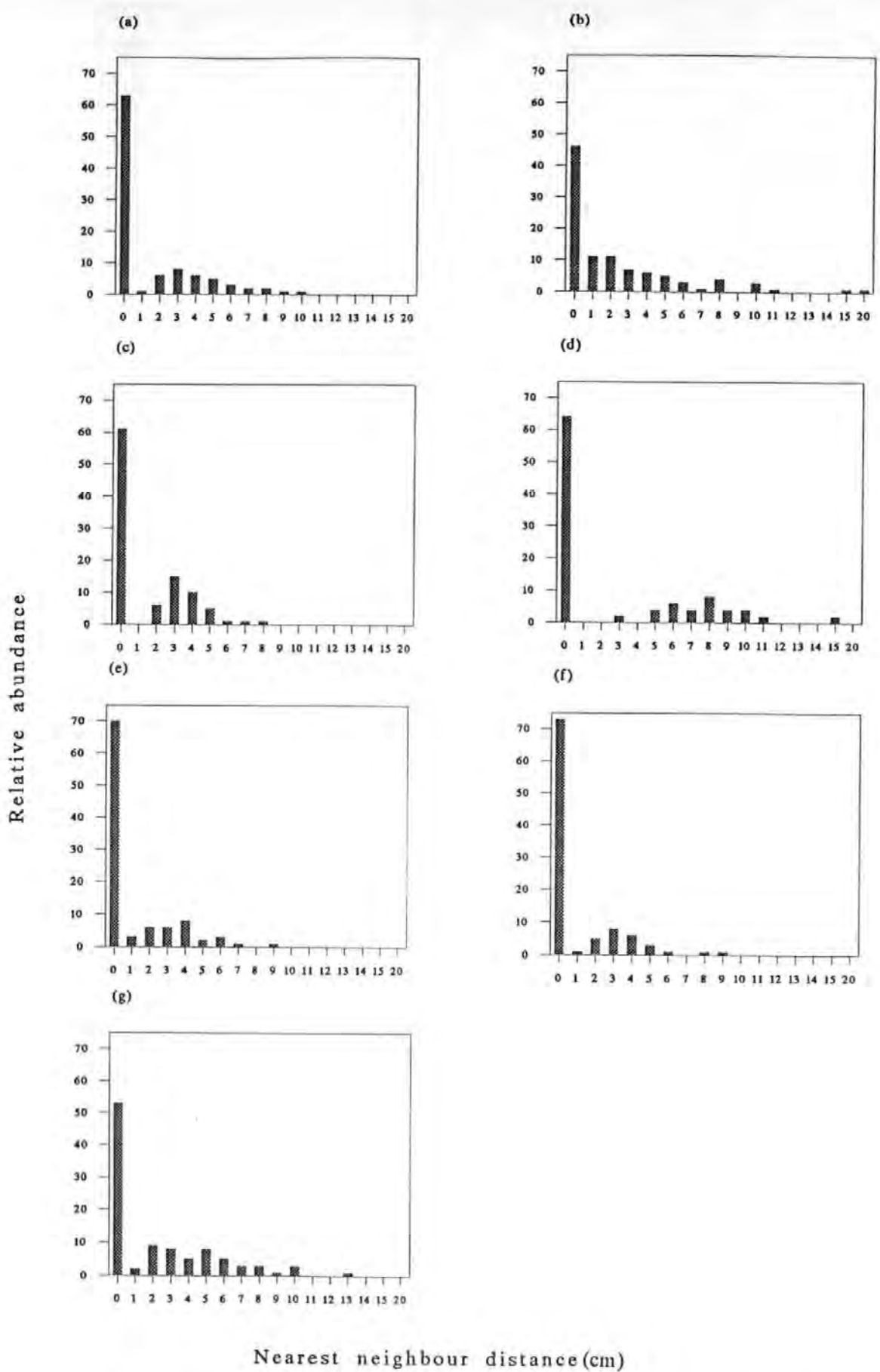
Figure 4.10: The relative abundance of nearest neighbour distances observed in 1994 in (a) the whole of Andrew's Wood, (b) Redlake, and within Andrew's Wood (c) the grazed area of compartment C, (d) ungrazed compartment C, (e) grazed compartment D, (f) ungrazed compartment D and (g) compartment A8.

(c)

NND (cm)	0	1	2	3	4	5	6	7	8	9+
Observed	50	14	39	58	61	42	41	16	19	129
Expected	252	10	42	39	22	42	22	16	16	19

Compartment A8 in Andrew's Wood 1994. $\chi^2 = 907$, d.f. $= 9$, $P < 0.001$.

(d)

NND (cm)	0	1-3	4+
Observed	14	26	29
Expected	42	14	13

Compartment C (grazed census quadrats) in Andrew's Wood 1994. $\chi^2 = 49$, d.f. $= 2$, $P < 0.001$.

(e)

NND (cm)	0	1-3	4+
Observed	19	40	2
Expected	50	8	11

Compartment D (grazed census quadrats) in Andrew's Wood 1994. $\chi^2 = 147$, d.f. $= 2$, $P < 0.001$

Table 4.5: Observed and expected number of *L. urens* seedlings emerging at increasing distance from neighbouring plants

A gap in the sward was a more favourable habitat than closed sward for the emergence of *L. urens* seedlings (Table 4.5). Nearest neighbour distance (NND) was strongly associated with emergence across Redlake and the whole of Andrew's Wood in 1994 (Table 4.5), although there were insufficient seedlings to test for association in the ungrazed census quadrats. There were fewer emergers beneath closed sward (i.e. NND is 0cm) and in A8, the only compartment with sufficient large gaps to separate out the remaining distance classes statistically, the larger the

gap the more seedlings were recorded than expected (Table 4.5c).

4.3.3 *Experimental seed bed*

The seed bed experiment was designed to allow an analysis of all the possible interactions of the four micro-habitat factors using a nested parametric ANOVA. The unexpected result of seedlings emerging from only fifteen percent of the plots meant that this analysis could not be employed. An ANOVA assumes data are normally distributed and it was not possible to transform the binomially-distributed data to give a normal curve because of the large number of zeros (empty plots). Due to these statistical difficulties, a two-sample Mann-Whitney U was used to show no significant difference in the blocks (test statistic, $Z = -0.43$). The blocks were then combined to show that germination was restricted to four micro-habitats, the most favourable of which were those with soil surface depressions alone (Plate 4.2, Table 4.6). Adding shade over depressions impaired emergence.

An interesting effect was seen in the positioning of seedlings within the plots. Although soil surface depressions appear to be necessary for germination, when the micro-habitat is shaded, seedlings emerge on the flat surface around depressions (Figure 4.11).

(a)   (b)
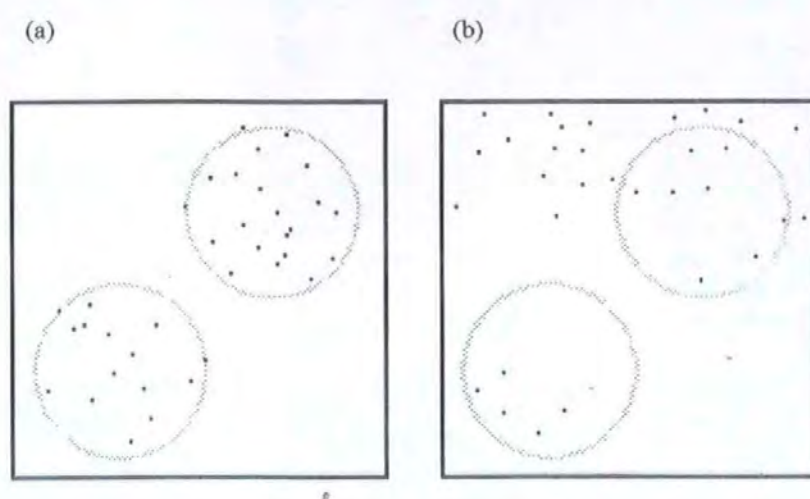
Figure 4.11: Map of seedling emergence in plots with two depressions and no litter or moss (a) unshaded, (b) shaded.

Plate 4.2: Emergence restricted to soil surface depression

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Micro-habitat				Number
S	M	L	D	emerging
1	1	1	2	0
1	1	1	1	0
1	1	1	0	0
1	1	0	2	0
1	1	0	1	0
1	1	0	0	0
1	0	1	2	0
1	0	1	1	0
1	0	1	0	0
1	0	0	2	40
1	0	0	1	34
1	0	0	0	0
0	1	1	2	0
0	1	1	1	0
0	1	1	0	0
0	1	0	2	0
0	1	0	1	0
0	1	0	0	0
0	0	1	2	0
0	0	1	1	0
0	0	1	0	0
0	0	0	2	52
0	0	0	1	43
0	0	0	0	0

Table 4.6: Showing total seedling emergence under differing soil surface micro-habitats simulated, in a seed bed, from the presence (1) or absence (0) of all combinations of four surface types (S = shade, M = moss, L = litter, D = depressions).

4.4 Discussion

The very high optimum germination temperature of *L. urens* suggests that it is better suited to more southern climes: germination temperature is, thus, at least partly responsible for restricting

the distribution of *L. urens* in Britain. Even on the low-lying land along the south coast of England, where the minimum temperatures required for germination are met, the percentage of seed able to germinate below 23°C is very low and the germination rate is slow. Germination success under the British climate is poor compared to that characteristic of central Spain.

Temperature is probably the main factor restricting germination to the period between March and November at the two reserves in southwest England. The average daytime air temperature during December and January, 9.4°C (unpublished Plymouth meteorological office data, 1970-1995), is well below the minimum constant temperature for germination (14°C). Within this time, when temperature is amenable, the seasonal diphasic germination in compartment A8, summer and autumn, could be a result of the lack of an after-ripening requirement for *L. urens* seeds. Thus, the first pulse is seed from previous years which finds itself on suitable sites and germinates as soon as the temperatures are high enough (May-June). This "old" seed at the soil surface is expended and there is then a lull in germination. The second pulse occurs from fresh seed immediately after dispersal (August-October) and tails off as temperatures fall. A possible suggestion as to why this phenomenon should occur only in compartment A8 would be that autumn grazing in compartments C and D removed the second cohort through regular trampling. At Redlake, regular trampling prevented spring seedlings from surviving long enough to be recorded in the fortnightly census. No recruitment was observed whilst ponies were grazing the reserve, but only a fortnight after the animals were removed, recruitment rates soared. The only major environmental change in those two weeks was the removal of the ponies.

There is an alternative hypothesis for the two cohort phenomenon seen in A8 of Andrew's Wood based on the requirement of *L. urens* seeds for a high soil moisture content. This was first suggested in Chapter 2 and is further supported by results from this chapter which show that germination is little impaired when seeds are fully immersed in water. The lull in germination over late summer could be a response to reduced soil moisture status, which would be more marked in the drier sheltered compartment A8. The distinct edaphic climate of A8 also offers

an explanation for the huge peak in emergence seen in the compartment in 1994 that could be a result of the drier, more sheltered soil reaching a critical temperature in the warmer summer of that year, which might override the lack of water in the soil.

In the seed bed experiment, germination was restricted to surface depressions. This could also be attributed to a need for a moist environment, since the depressions brought seed closer to the water source, reduced soil insolation and air flow and thus kept humidity and soil moisture higher than on a flat surface (Sheldon, 1974; Harper, 1977; Eldridge *et al.*, 1991). Similar seed bed experiments to investigate the effect of heterogeneity in soil surface microtopography on germination were carried out by: Harper, Williams & Sagar (1965), who worked on three *Plantago* species; Sheldon (1974), who studied a range of Compositae; and Smith & Capelle (1992) who used *Cichorium intybus*. Each found that those microtopographical features which protected against moisture loss, e.g. depressions, plastic or polythene strips, had the most pronounced increase in percentage germination. The reason why the favourability of depressions in the seed bed was not reflected in the field is unclear. The dimension of depression which provides favourable conditions may be critical. Thus field depressions which were too large would have weakened the relationship.

There is a paucity of information on the effects of bryophytes on vascular plants, but there have been observations of a change in germination or emergence success of vascular species in bryophyte colonies (During & van Tooren, 1990). More successful emergence within bryophyte colonies has been reported in harsh environments such as dunes (Bonnot, 1971) and desert crusts (St Clair *et al.*, 1984), whereas reduced emergence was found in communities more similar to that associated with *L. urens* i.e. grassland (Rabotnov, 1969) and heath (Mallick *et al.*, 1984). In this field study, the presence of a moss layer increased the emergence of *L. urens* seedlings. The most likely mechanism responsible for this is the moisture retentive quality of mosses (Johnson & Thomas, 1978; Chernov, 1985). An indirect facilitative effect could be occurring, since bryophytes occupy the 'niche space' that is left by vascular plants (Looman,

1964) which inhibit emergence (see below). A previous study found seeds of *Cerastium semidecandrum* L. suffered less predation in taller moss colonies (*Hypnum cuppressiforme* Hedw. and *Campylopus introflexus* (Hedw.) Brid.) than in lower turf species or on bare ground (During & van Tooren, 1990). The seeds of *C. semidecandrum* are 0.4 mm - 0.5 mm long (Clapham *et al.*, 1987), which is a similar size to those of *L. urens*. It is less likely that *L. urens* seeds would be protected by *Rhytidiadelphus squarrosus* (Hedw.) Warnst. and *Pseudoscleropodium purum* (Hedw.) Fleish., the most common species at Andrew's Wood and Redlake, since these are pleurocarpous and occurred as scattered stems rather than acrocarpous tall cushions. Moreover, it is not believed that predation is a major limiting factor to such small-seeded species (Janzen, 1969; Silvertown, 1982; Crawley, 1983; Fenner, 1985). The growth form of the two dominant moss species could help to explain why moss was facilitative to *L. urens* (following Rabotnov, 1969; Mallick *et al.*, 1984). The germination of *Rhododendron ponticum* L. in Irish woodlands was seen in micro-habitats with scattered strands but not in the presence of an excessively thick moss layer, which reduced the light levels considerably (Cross, 1981).

The positive effect of moss on germination observed in the field was not repeated in the seed bed experiment. The effect of moss in the seed bed resembled that of litter, since it did not establish itself, was not living and therefore it provided neither sufficient increase in soil moisture nor indicated open areas devoid of higher plants.

It has been reported in other studies that micro-habitat quality over-rides the effects of neighbouring juveniles on germination (Fowler, 1988; Donovan *et al.*, 1993). This appeared to be the case in this study, with the density of seedlings increasing in response to the size of the gap in the sward, measured as the distance to the nearest neighbour. However, the critical density to cause self-thinning may not have been reached. The germination of *L. urens*, like many plant species (Sagar & Harper, 1961; Putwain & Harper, 1970; Gross, 1980), was improved by an opening in established vegetation. In this study, the quality of the opening was

seen to be important with a greater density of seedlings emerging in larger gaps in the sward. Goldberg & Werner (1983) did not find such a straight-forward relationship between gap size and emergence for their two *Solidago* species, but they did report significant rank correlation between percentage survival and opening size that they attributed to the effects of canopy-filtered light. The shading in the seed bed experiment reduced, but by no means halted, germination. This neutral seed bed shading mimicked the quantity of light present at ground level in the field but did not reduce the light quality as plant cover does. The lower light intensities caused by a combination of litter and canopy shade may have inhibited germination below higher plant cover in part. However, there are very low red to far-red ratios beneath the swards of Andrew's Wood and Redlake (Figure 6.13) and results from the seed bed suggest that it was the quality of light that suppressed germination in the field. The restricted germination of *Lolium multiflorum* (Deregibus *et al.*, 1994), *Anthyllis vulneraria* and *Reseda lutea* (Silvertown, 1981) beneath a closed sward has been at least partly attributed to phytochrome perception of low red to far-red ratios.

Seed germination has been studied in several species of lobelia with special emphasis on the light requirement. In addition to *L. urens*, other lobelias have been found to have a light requirement for seed germination. The seeds of *L. inflata, L.siphililica, L. cardinalis* (Muescher, 1936) and *L. gattingeri* (Baskin & Baskin, 1979) failed to germinate when incubated in darkness. However the seeds of *L. dortmanna, L. erinus* and *L. tenuior* germinated equally well in light and continuous darkness (Muescher, 1936).

Cover by higher plants affects other environmental factors besides light. Fenner (1978) suggested that a requirement for alternating temperatures may restrict germination in the closed sward but since *L. urens* does not require alternations to induce germination, this is not the case. Competition for moisture is a more likely restriction for a species suited to high soil moisture conditions; even the slightest water tension restricts the germination of the corn-cockle (*Agrostemma githago*) (Harper & Benton, 1961). A further negative effect could be induced by

higher plant cover indirectly through the production of leaf litter.

In this experiment, there was a lack of recruitment beneath *Molinia caerulea* litter, both in the field and the seed bed. Hence a safe site for *L. urens* must be free, or almost free, of litter. As mentioned above, this negative effect of litter may be partly caused by a reduction in the light intensity but litter is often inhibitory through other effects (see Facelli & Pickett 1990 for a review). Even a sparse scattering of litter, insufficient to cover the surface, significantly reduced the survival of seedlings of two grass species, *Aristida longiseta* and *Boulesova rigidiseta* (Fowler, 1988). Litter may reduce germination by obstruction of the dispersal of seed to the soil surface (section 7.3) and by restriction of soil-to-seed contact (Andersen, 1967; Fowler, 1988). In addition to the changes to the physical environment brought about by litter, there are the secondary effects induced by its presence as well as the physiological effects exerted by its decomposition. These include the increase in both invertebrate damage and pathogen attack (Eldridge *et al.*, 1991; Facelli, 1994), the immobilisation of plant nutrients and the production of phytotoxic by-products (Harper, 1977; Rice, 1984; De Jong & Klinkhamer, 1985; Pastor *et al.*, 1987; Bosy & Reader, 1995). Litter has been seen to be favourable to the germination and establishment of some species, since it alters the thermal amplitude of the soil by intercepting solar radiation and by acting as an insulator. Litter also increases soil moisture by reducing evaporation (Knapp & Seastedt, 1986; Holland & Coleman, 1987). However, for small-seeded species like *L. urens*, the presence of litter usually hinders germination (Molofsky & Augsperger, 1992). Baskin & Baskin (1979) attributed the failure of *Lobelia gattingeri* seeds to germinate to the presence of the litter of *Sporobolus vaginiflorus*, an annual grass, on the soil surface.

Historical records of dramatic increases in the size of several populations in response to soil disturbance (section 2.2) is likely to be a result of bringing the dormant seeds out of the bank (Harper, 1977). *L. urens* does not respond to diurnally fluctuating temperatures, unlike most small-seeded wetland species, which form persistent seed banks and are thought to respond to

disturbance (see Thompson & Grime, 1983; Leck, 1989; Thompson, 1993c). Thus, it is not a requirement for alternation that suppresses germination in the soil. The light requirement of *L. urens* seed enforces dormancy in the soil and permits the formation of a large persistent seed bank; a common trait in small-seeded species (Grime *et al.*, 1981; Pons, 1992). To germinate, the seed must somehow be brought to the surface to expose it to the light. The lack of recruitment in the ungrazed quadrats at Andrew's Wood and Redlake, other than after heavy grazing, could be a result of the immobility of seeds in the bank through lack of poaching and soil disturbance. The results described from these experiments suggest two further means by which grazing can increase the percentage germination of *L. urens*: first, by creating gaps in the vegetation through poaching and defoliation, which improve the light and moisture environment for germination; and second, through disruption of the litter layer and subsequent incorporation of the litter into the soil, removing its many deleterious effects. Both these processes enhance emergence and it is often difficult to separate them in the field (Hobbs & Huenneke, 1992).

The soil compaction produced by poaching often poses a problem for germination (Scholefield & Hall, 1985). Sheldon (1974) saw that a weight dropped onto a pot compacted the soil and reduced the germination of Compositae species by homogenizing the surface topography and thus removing the safe sites. Compaction may have been minimal in the wet soil of Andrew's Wood and Redlake, or insufficient to outweigh the advantage of increased soil moisture. The latter is more likely, since there is some evidence that water-filled pores are no more resilient to compression than air-filled (Scholefield, 1986).

Over two years, this study has shown sensible, consistent relationships between seedling emergence and microhabitat. Other recent work on safe sites showed the recruitment of *Atriplex vesicaria* varied significantly between different categories of soil surface micro-environments but with no consistency between cohorts as to which habitat supported the greatest emergence (Eldridge *et al.*, 1991). Similarly, the emergence of two grasses, *Aristida longiseta* and *Boulesova rigidiseta*, varied in a complex fashion between years, cohorts and species

(Fowler, 1988). This could be because those relationships which change between years and cohorts depend upon fine-scale seasonal changes in environment. For example, in a dry season, habitats which help retain soil moisture may be favourable, whereas in a cool year, temperature might override a moisture requirement. There was some evidence of complexity in the emergence patterns of *L. urens* but its relationship with micro-habitat was more robust. At the northern extreme of its distributional range, whatever the weather, a combination of higher temperatures with more soil moisture would improve the germination success of *L. urens*.

FIVE

The fate of seedlings
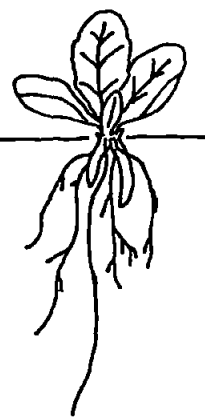
5.1 Introduction

The germination of *L. urens* in Britain is restricted by the need for a moist environment combined with high temperatures. Light is also a requirement; seeds must be brought out of the bank onto bare soil. Both living and dead plant material inhibit the emergence of *L. urens*. In spite of these controls on the germination of *L. urens*, plant distribution and abundance is determined largely by the number of seedlings which establish (Harper, 1977; Grubb, 1977; Reader, 1993). The seedling stage is the most vulnerable time in the life cycle of a plant (Darwin, 1859; Harper, 1977; Caver, 1983), because seedlings have few reserves to call upon in the face of unfavourable conditions (Angevine & Chabot, 1979). The comparatively small seeds of *L. urens* contain minimal energy reserves and this increases the plant's vulnerability during the establishment phase.

Seed size affects many aspects of a plant's ecology (Schimpf, 1977). Positive correlations between seed size and seedling size have been demonstrated for a number of monocarpic perennials (Gross, 1984) along with *Calamoulfa longifolia* (Zhang & Maun, 1993) and *Virola koschynyi* (Gonzalez, 1993). Correlations have also been found between seed size and the growth rate of seedlings of *Rumex crispus*, *Rumex obtusifolius* (Cideciyan & Malloch, 1982), *Rumex acetosella* (Houssard & Escarre, 1991) and *Raphanus raphanistrum* (Stanton, 1984). Through its effect on seedling vigour, seed size influences the hardiness of seedlings to perturbations (Grieve & Francois, 1992; Maun, 1994) such as defoliation (Russi *et al.*, 1992; Armstrong & Westoby, 1993) and cover by litter (Vazguez & Orozco, 1992). Smaller seeded species, *Verbascum thapsus* and *Oenothera biennis*, showed poorer establishment in vegetated cover than on bare soil (Gross, 1984) and similarly the sensitivity of seedling growth to shading

was significantly negatively correlated with the mean seed reserve weight for twelve rain forest species in northern Queensland (Osunkoya *et al.*, 1994). Small seed size is generally assumed to competitively disadvantage seedlings (Harper *et al.*, 1970; Baker, 1972; Howe & Richer, 1982) and one of the most obvious disadvantages may be in drought tolerance. A large number of small-seeded species are especially vulnerable to drought (Schimpf, 1977; Evans & Etherington, 1991; Leishman & Westoby, 1994a), a phenomenon which is of particular interest to this research, since all extant British populations of *L. urens* are situated in the lowland regions of the southern coastal counties, on soil which is prone to winter waterlogging (section 2.6).

Lack of the specific habitat required for establishment has been cited as the major limiting factor in a number of rare plant species. For example, *Orothamnus zeyhers*, a montane species, restricted to seventeen sites on the cape of South Africa, requires open areas created by burning to rejuvenate (Boucher, 1981), while the average establishment success from seedlings of *Peucedanum palustre*, a fenland species which is very rare in Britain, was less than one percent, since it can only establish successfully in areas that have been recently cut (Meredith, 1978). In this study, seedling size and survival were used to measure the degree of favourability of different environmental conditions and micro-habitats to establishment. Initially, there were three aims. First, to determine the relationships between germination date and seedling success at Andrew's Wood and Redlake. Second, to identify the favourability of the various micro-habitats at the two reserves and under the experimental conditions of a seed bed, especially the moss layer and soil surface depressions, which are beneficial to germination (section 4.3.3). The third aim was to investigate the effect of moisture and frosting on establishment in laboratory studies, in order to relate the results to the demographic patterns of survival in the field and to the national distribution of *L. urens*.

5.2 Methods

5.2.1 *Field demography*

The survival of seedlings which emerged in the census quadrats was monitored as part of the fortnightly census described in section 3.3.2, while the method used to record the micro-habitat of these seedlings is outlined in section 4.2.2.

5.2.2 *Experimental seed bed*

The design of the seed bed is described in section 4.2.3. The survival of seedlings which emerged from the bed was followed every other day from June 6 to July 23, 1994.

5.2.3 *Response to waterlogged conditions*

Seed taken from the pool collected in autumn 1993, as described in section 4.2.1, was sown on May 3 1994 into forty compartment seed trays filled with sterilised soil from Andrew's Wood and germinated in an unheated glasshouse. The soil was kept moist and, following germination, seedlings were thinned to one individual per compartment. Seedlings were grown on until 28 days old, when the second true leaf was beginning to show, to guarantee that the experimental effect was exerted on the establishment phase and not on germination. The two treatments used were developed from Voesenek *et al.* (1993). The trays were arranged in a latin square on the centre bench of a glasshouse to incorporate variability in the light and temperature environment. The waterlogged plants were submerged in water to soil surface height and the water was changed weekly. Plants under the damp treatment were watered from above twice a day and more frequently when necessary. In total, 120 plants were exposed to each treatment. Twelve seedlings, chosen at random, were removed from each treatment every five days and placed in a recovery area, where they were watered from above, twice a day, and more frequently when necessary.

The experiment ran for 50 days, after which plants were removed from the soil; seedlings were then 78 days old. The number of survivors was recorded, roots were washed and plants dried at 80°C in a fan oven for 24 hours. After allowing to cool in a desiccator, dried plants were separated into roots and shoots. All handling was performed using forceps to prevent any moisture from the hands affecting the final weights. The dry weight was determined using a Sartorius 2001 MP2 balance.

5.2.4 *Response to frosting*

Seed taken from the pool collected in autumn 1993, as described in section 4.2.1, was sown on March 15 1995 in 40 mm diameter pots filled with John Innes No. 2 and germinated in a Sanyo MIR-152 incubator at 29°C. Following germination, treatments developed by Thorpe, Hendry & Duran (1993) to test plant response to short incidents of low temperature were used and were adapted to investigate the lethal low temperature for *L. urens*. Five replicate plants for both treatments were grown in an unheated glasshouse under a 14 hour day at 25°C and a 10 hour night at 15°C (range ±3°C). The pots stood in 10 mm of water which was changed weekly. Five control plants were maintained under these conditions throughout. At 21 days old five plants were exposed to three days at 14°C:9°C (day:night), followed by four days at 5°C:1°C. These chill-stressed plants were then returned to the glasshouse. At 21 days old five plants were exposed to two days at 14°C:9°C (day:night), followed by two days at 5°C:1°C, three days at 2°C:-2°C, and finally two days at 14°C:9°C. These freeze-stressed plants were then returned to the glasshouse (Thorpe, Hendry & Duran, 1993). After exposure, all plants were grown on until 42 days old, then harvested using the same method as for the waterlogging experiment. The dry weight was determined using a Cahn 29 automatic electrobalance.

To identify the lethal low temperature, two replicates were exposed to each of the adapted freezing regimes. The first substituted -4°C nights for -2°C nights and the second lowered this to -6°C. After exposure, the plants were grown on until 50 days old and the damage assessed visually.

5.3 Results

5.3.1 *Field demography*

Over the two years the fate of 1087 seedlings was monitored at Andrew's Wood and of these, nineteen, 1.75%, survived to flowering (Table 5.1). None of the 65 seedlings which emerged in the monitored area at Redlake survived for more than two months.

	1993		1994	
	Emerge	Survive	Emerge	Survive
January	-	-	1	0
February	-	-	0	0
March	19	4	14	1
April	63	2	60	0
May	55	1	181	0
June	91	3	199	3
July	38	1	86	4
August	54	0	46	0
September	28	0	26	0
October	28	0	60	0
November	23	0	15	0
December	0	0	-	-

Table 5.1: Monthly survival success of *L. urens* seedlings emerging from the period March 1993 to November 1994 at Andrew's Wood

Seedling survival was too low to compare the establishment success of individual monthly cohorts or compartments within Andrew's Wood (Table 5.1). In both years, however, there was a clear bisection with a low establishment success from March to July (early), whilst no seedlings established August to February (late). This consistency meant seedlings could be categorized across the years into a early and a late cohort, that gave sufficient counts to perform a chi-square test for association (Table 5.2). The null hypothesis that there was no association between survival and cohort was rejected, $P < 0.05$ with Yates correction.

	Survival to adult		
	+	-	
Early cohort	**19** (14)	**787** (792)	**806**
Late cohort	**0** (5)	**281** (276)	**281**
	19	**1068**	**1087**

Table 5.2: Chi-square test for association between emergent seedlings survival to adult and seasonal germination cohort. Observed values in bold, expected values in brackets. $\chi^2 = 5.4$, d.f. = 1, $P < 0.05$.

Determining the fate of seedlings presented formidable problems. A large proportion simply disappeared in the intervals between monitoring and may have been eaten (Andersen, 1989), washed away or trampled into the soil. Even when there were shrivelled remains, it was impossible to assign a cause of death; drought, grazed roots, disease or even genetic defect were all possibilities (Fenner, 1987).

Figure 5.1 shows that the initially very steep survival curves levelled out, denoting that the probability of survival increased with seedling age. However, there did not appear to be a critical time of year or a common post-emergence period after which this improvement occurred (Figure 5.1).

The size of the plants might yield more information on their survival, since reaching a critical size can endow seedlings with an improved survival (Werner, 1975b). Plant size was monitored as part of the fortnightly census in terms of average leaf length and leaf number (section 3.3.2). The medians of each monthly cohort showed similar trends over time but leaf length gave a smoother curve because, within the gradual increase in size described by the curves, there was a fluctuation caused by the death of plants. The loss of a number of relatively small plants between censuses caused a sharp rise in the median, whereas the death of large plants could result in a sudden drop (Figure 5.2). Median leaf length was more robust against the fluctuations and was therefore a more useful measurement of plant size. Individuals were

categorised on the basis of flowering in first year, since flowerers and non-flowerers had such different size curves (Figures 5.3 & 5.4). The slope of the size curves provided a measure of growth rate. There appeared to be no consistency between the initial growth rate and the survival of cohorts (Figures 5.1 & 5.3), however, the slopes of the curves were still partially obscured by the fluctuations. In the initial stages, these fluctuations were caused by the large numbers of deaths (Figure 5.1) and latterly, they were a function of the small sample size, since cohorts were often reduced to less than five individuals. In general, relative growth rates brought to bear on the total dry weights of the plants provide a far more informative comparison of the plants' performance than size alone (Hunt, 1982). However, such calculations require destructive sampling, which was not feasible in this field study. Converting the direct measurements of leaf length that were obtained into a relative growth rates would not have provided more information than these size curves.

Of the 1087 seedlings monitored over the two year period, only 1% reached flowering in their first year. These nine plants originated from the March, April and May cohorts in both 1993 and 1994 and reached a much larger size than those which remained vegetative throughout their first year (Figures 5.3 & 5.4). Of those remaining vegetative, the earlier cohorts, given a longer growing season, reached a larger size (Figures 5.2 & 5.3).

The growth curves of the flowering individuals differ in shape between years. In 1993, plants of the three cohorts reached a similar size, peaking in August then senescing during October, whilst being replaced by new rosettes. Although the April cohort of 1994 had a similar curve to this, the March cohort reached their maximum size earlier in July, senesced through August and September and thus there was a short period with no visible above ground tissue before new rosettes budded from the rhizome in October. The individual which emerged in May 1994 and flowered in its first year died in the October.

Seedlings survived to adulthood in only four of the seven habitats favourable to emergence (Table 5.3). Habitats with only moss or with moss and ground cover by higher plants were

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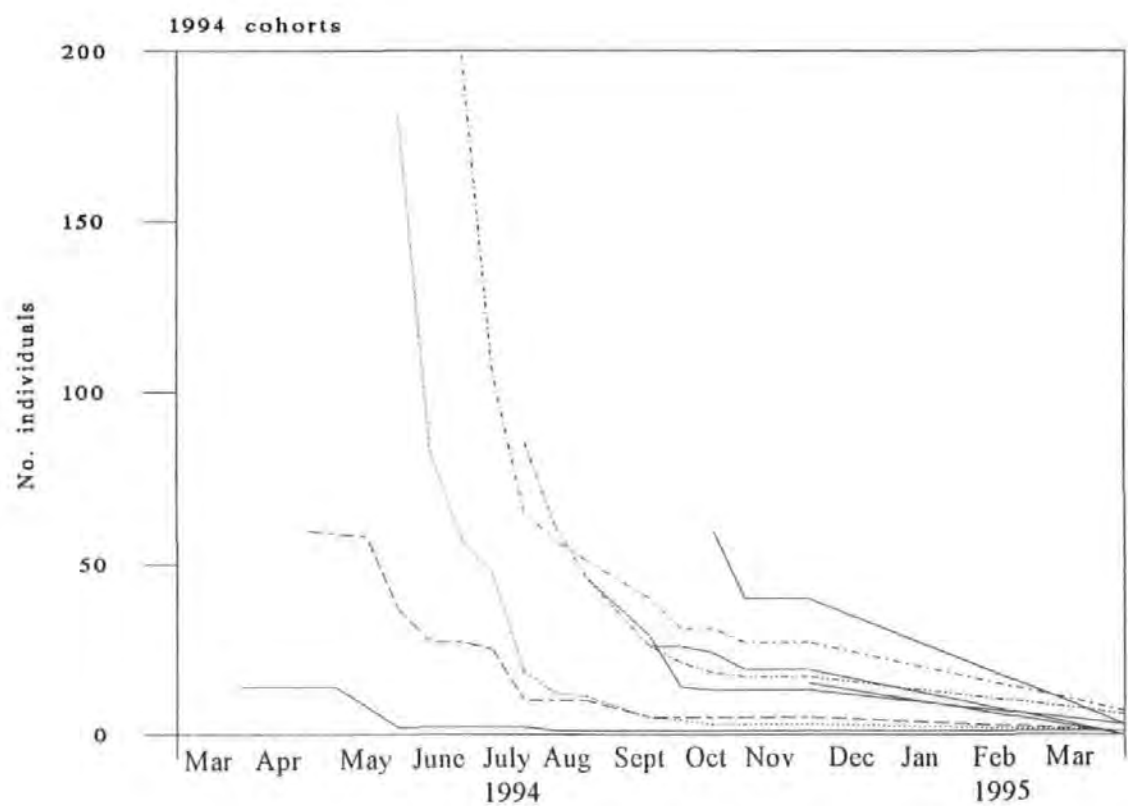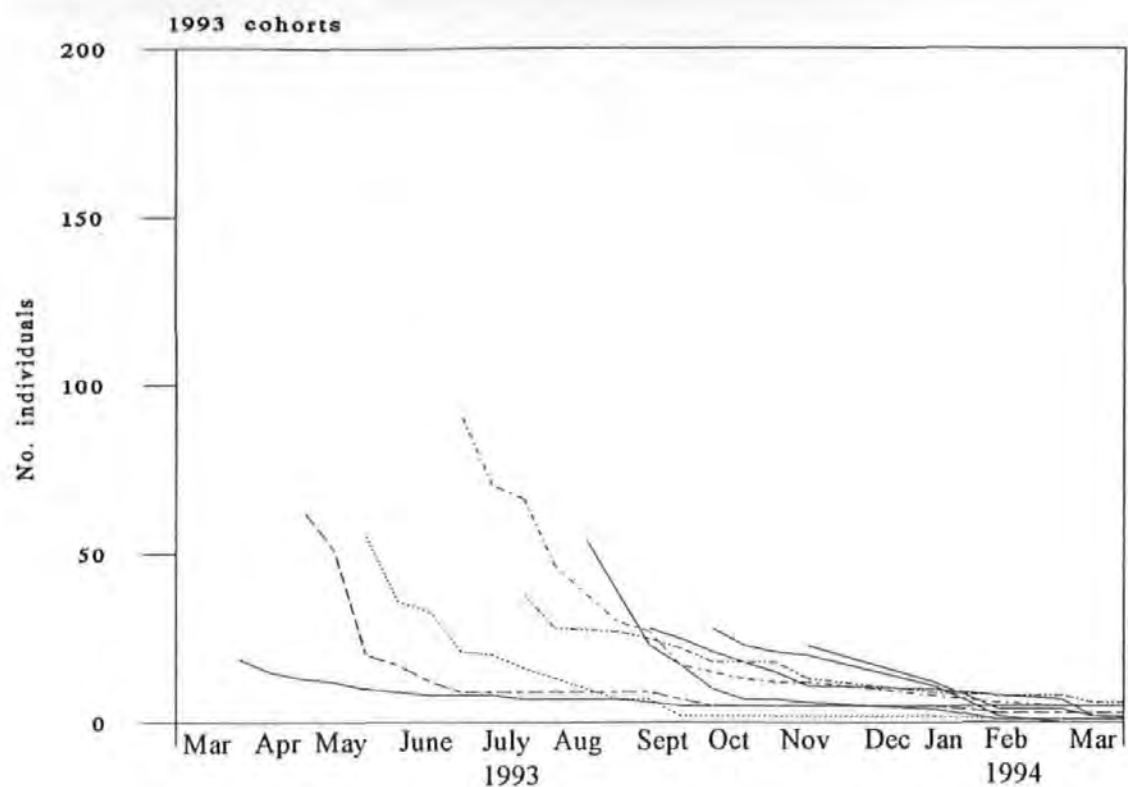
Figure 5.1: The survival of monthly cohorts at Andrew's Wood 1993 and 1994.

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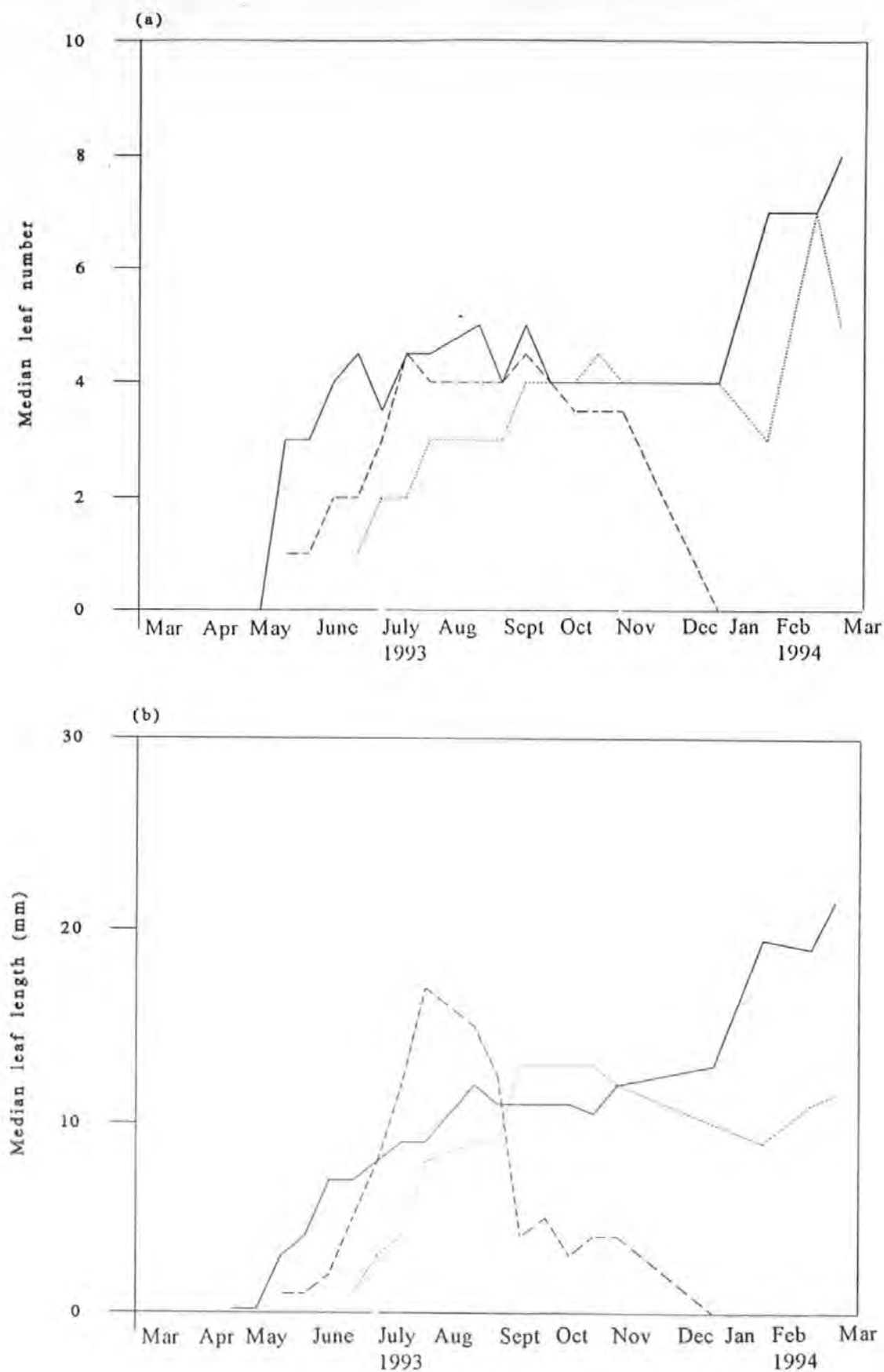
Figure 5.2: A comparison of size curves of plants that emerged at Andrew's Wood in the months of April (solid line), May (long dashes) and June (short dashes), expressed as (a) total number of rosette leaves and (b) average leaf length.
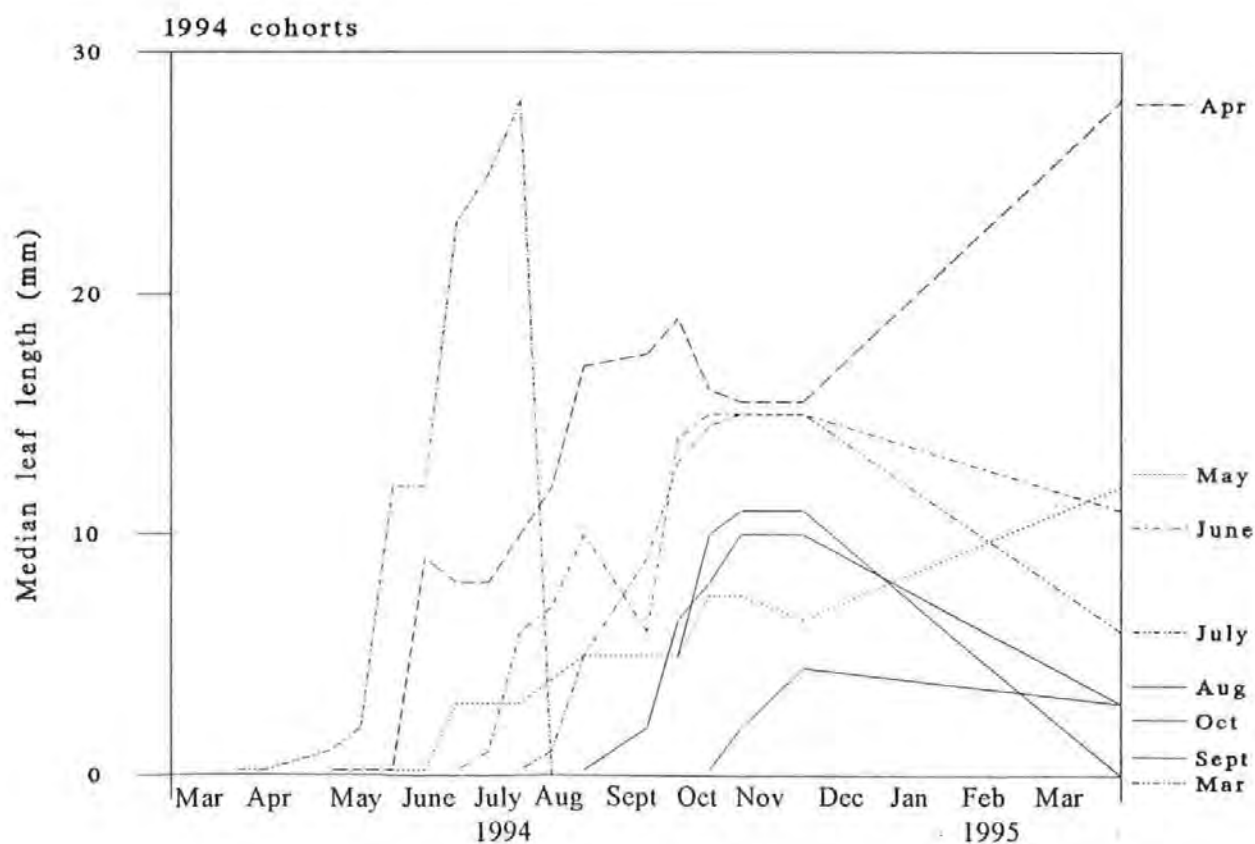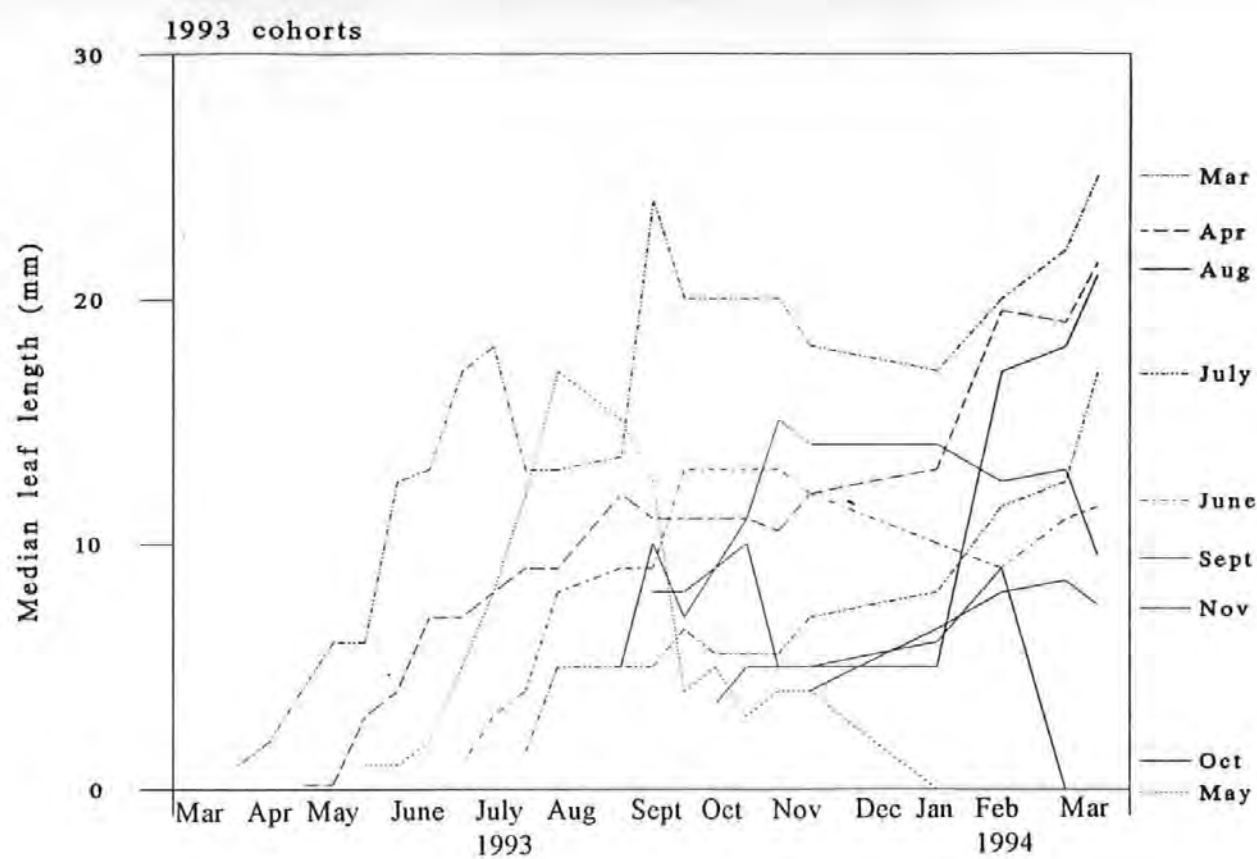
Figure 5.3: Size curves of plants from Andrew's Wood remaining vegetative in their first year, 1993 and 1994.
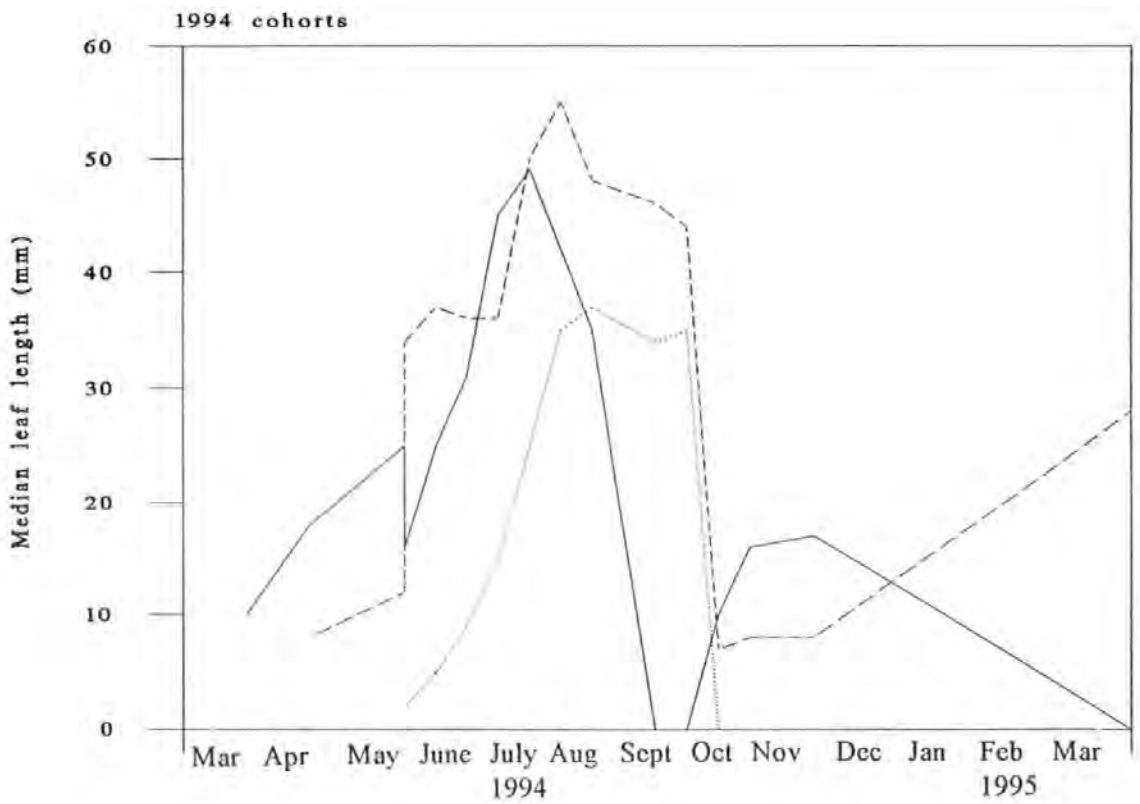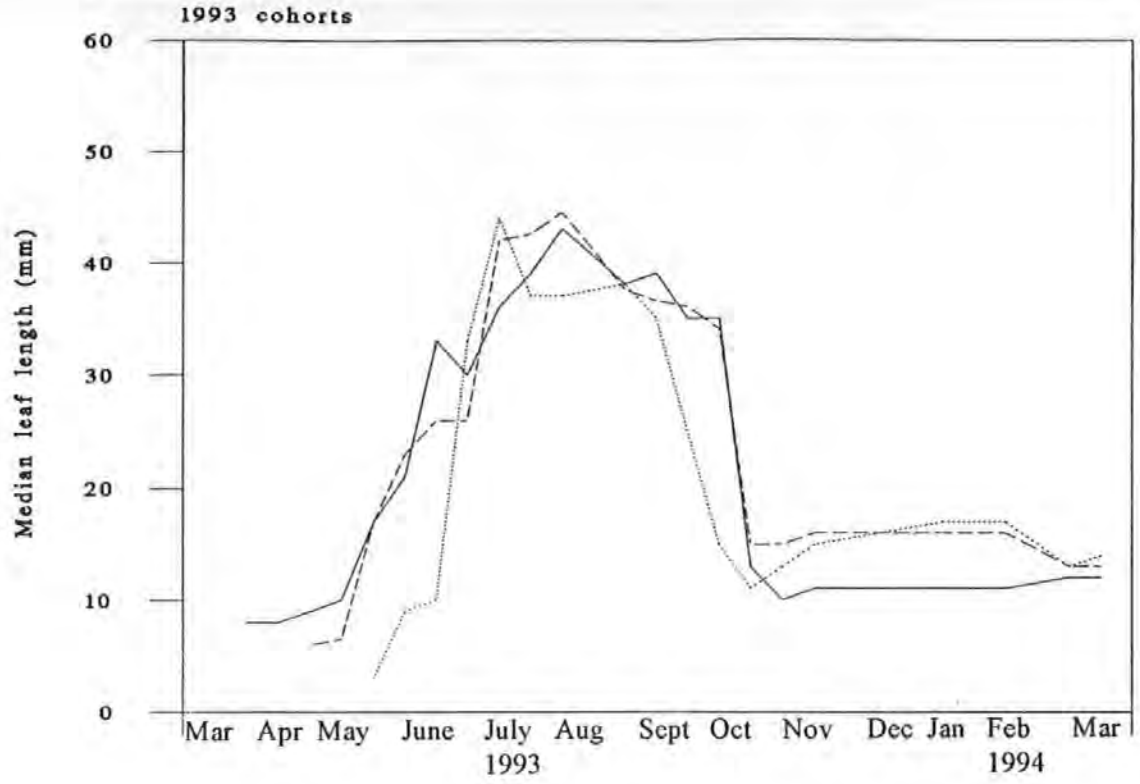
Figure 5.4: Size curves of plants flowering in their first year that emerged at Andrew's Wood in March (solid line), April (long dashes) and May (short dashes), 1993 and 1994.

G	M	L	D	Habitat availability 1994-95	AW93			AW94			Habitat rating
					Emerge counts	Survival counts	% survival	Emerge counts	Survival counts	% survival	
1	1	1	1	0.000	0	0	0	0	0	0	
1	1	1	0	0.018	4	0	0	34	0	0	
1	1	0	1	0.000	0	0	0	0	0	0	
1	1	0	0	0.005	12	1	8	14	2	14	✓✓★
1	0	1	1	0.000	0	0	0	0	0	0	
1	0	1	0	0.477	5	0	0	18	0	0	
1	0	0	1	0.000	0	0	0	0	0	0	
1	0	0	0	0.141	0	0	0	17	0	0	
0	1	1	1	0.010	66	2	3	18	1	6	✓✓
0	1	1	0	0.083	154	3	2	222	2	1	✓✓
0	1	0	1	0.008	17	0	0	14	0	0	✓
0	1	0	0	0.026	84	2	2	56	5	9	✓✓★
0	0	1	1	0.073	5	0	0	12	0	0	
0	0	1	0	0.129	25	0	0	209	0	0	
0	0	0	1	0.001	6	0	0	18	0	0	✓
0	0	0	0	0.031	21	0	0	56	0	0	✓

Table 5.3: Survival to adult under differing soil surface micro-habitats produced from the presence (1) or absence (0) of all combinations of four surface types (G = ground cover by higher plants, M = moss, L = litter, D = depression) at Andrew's Wood 1993-1994. Micro-habitat key rating (✓) favourable to emergence, (✓✓) favourable to emergence and survival, (✓✓★) show greatly improved emergence and survival.

most favourable (Table 5.3). No seedlings survived to become adults at Redlake in 1994 and only ten did so at Andrew's Wood. As a result of this very low survival rate, it was not possible to test statistically for an association between distance to nearest neighbour (NND) and survival. However, two of the ten censused seedlings to reach adulthood emerged in a closed sward (NND = 0).

5.3.2 Experimental seed bed

Four habitats facilitated the emergence of *L. urens* (Table 4.9). There was no significant difference in the survival success of seedlings between the two replicate blocks (two sample comparison, Mann-Whitney U, test statistic, $Z = 0.62$). Therefore, data from the two blocks were combined and a Kruskal-Wallis test used to look for differences between habitats. There was a difference between the four habitats in which seedlings germinated (Kruskal-Wallis, test statistic = 43.54, $P < 0.001$); survival followed the same habitat trend as suitability for germination. Soil surface depressions alone provided the most favourable habitat and survival was impaired by the addition of shading (section 4.3.3, Figure 5.5).
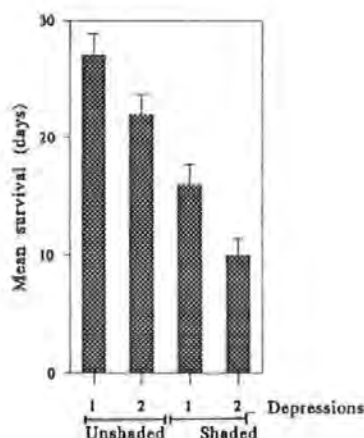
Figure 5.5: The mean number of days *L. urens* seedlings survived ($\pm$ 1 standard error of the mean) in the seed bed under shaded and unshaded micro-habitats with one or two soil surface depressions.

5.3.3 *Response to waterlogged conditions*

A waterlogged soil increased the dry weight gain of *L. urens* seedlings when grown under glasshouse conditions (Figure 5.6). Waterlogged seedlings were significantly larger than those kept damp (F = 31.19, P <0.001) (Table 5.4). The difference was manifested when seedlings were subjected to more than twenty-five days treatment (Figure 5.6). Both shoots and roots of waterlogged plants were significantly larger than those of the damp plants, however, the greatest difference was between the roots (F = 17.44 & F = 31.81 respectively).
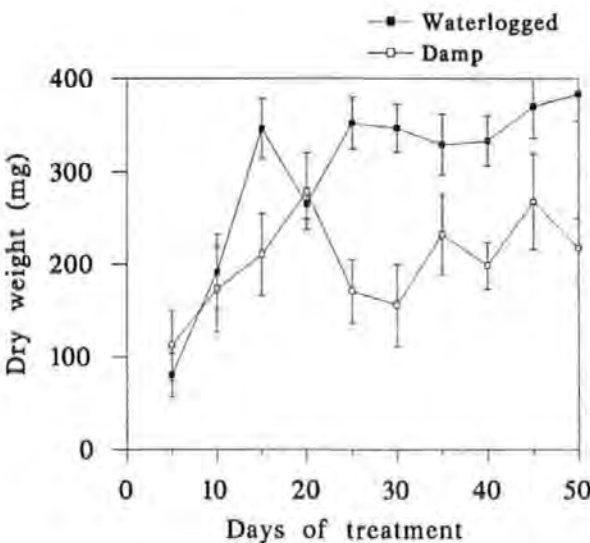
Figure 5.6: The mean change in dry weight (± 1 standard error of the mean) of *L. urens* seedlings maintained, over fifty days, under either waterlogged or damp conditions.

	d.f.	MS	F
Total dry weight	1	609739.20	31.19***
Dry weight of shoots	1	76398.02	17.44***
Dry weight of roots	1	234275.00	31.82***

*P < 0.05, **P < 0.01, ***P < 0.001

Table 5.4: Results of three one-way ANOVAs on the change in dry weight of *L. urens* seedlings maintained, over fifty days, under either waterlogged or damp conditions. Degrees of freedom (d.f.), mean squares (MS) and F-ratios are indicated.

5.3.4 *Response to frosting*

The total plant dry weight was significantly affected by chilling and by freezing (F = 24.77, P < 0.001) (Table 5.5). The roots showed significantly more damage than the shoots (F = 45.04 & F = 8.18 respectively) (Table 5.5, Figure 5.7). The lethal regime for seedlings was -6°C.
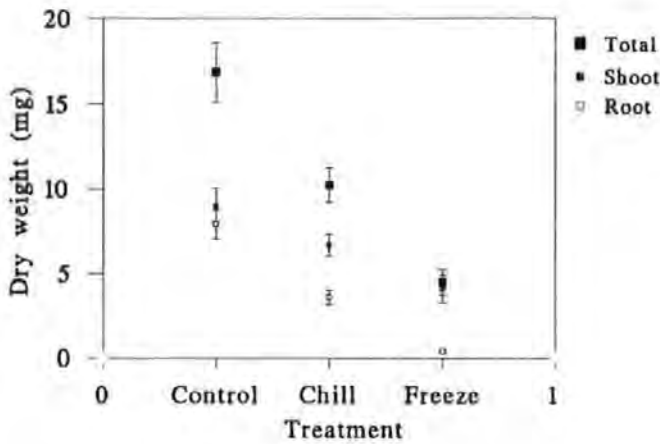
Figure 5.7: The mean dry weight (± 1 standard error of the mean) of *L. urens* seedlings after exposure to chilling and freezing regimes.

	d.f.	MS	F
Total dry weight	2	191.80	24.77***
Dry weight of shoots	2	29.84	8.18***
Dry weight of roots	2	70.73	45.04***

*P < 0.05, **P < 0.01, ***P < 0.001

Table 5.5: Results of three one-way ANOVAs on the effects of chilling and freezing regimes on the dry weight of *L. urens* seedlings. Degrees of freedom (d.f.), mean squares (MS) and F-ratios are indicated.

5.4 Discussion

The losses in dry weight shown by *L. urens* in response to short incidents of low temperature were most similar to those species of lowland cold-temperate latitudes (Table 5.6). The lethal regime for seedlings was -6°C, a temperature rarely experienced within the range of *L. urens* in Britain, but one frequent further north (Meterological Office, 1976). Therefore low temperature could be enforcing the northern distribution limit of *L. urens* within Britain, through seedling

establishment. Low temperature is one of the most limiting factors of natural plant distribution (Parker, 1963). Temperatures below -6°C are, however, common in the upland valleys of the Pyrenees and Montes de Toledo, where *L. urens* thrives (Brightmore, 1968). As adult plants are completely frost tolerant (Brightmore, 1968), it seems likely that factors such as the shorter growing season and lower summer temperatures (Pearce & Smith, 1984) limit establishment and growth rate at the northern edge of its range and thus *L. urens* seedlings do not reach the size necessary to withstand the low temperatures of winter.

The small compact seed of *L. urens* has improved dispersal (Thompson, 1993b) and persistence (Thompson, 1993a; Thompson *et al.*, 1993) (see section 7.3), rather than the superior establishment and growth associated with large seeds (e.g Howe & Richer, 1982; Cicidiyan & Malloch, 1982; Stanton, 1984; Waller, 1984). With less energy embodied in *L. urens* seed, large numbers can be produced which can compensate for the enormous wastage of individuals through inefficient establishment (Salisbury, 1975; Cavers, 1983). Considering this, the survival success of *L. urens* at Redlake and Andrew's Wood is still very low and it is likely to be contributing to restrictions on population size. At 3%, survival from germination was much lower than that recorded in demographic studies of three common species: *Medicago lupulina*, 47% (Parone & Reader, 1982), *Aristida longiseta*, 32-50%, and *Bouteloua rigidiseta* 38-65% (Fowler, 1988). Establishment success was even lower than that of *Orothamus zeyhers*, a rare montane species of South Africa whose rarity was attributed to a 'low' establishment of 10% (Boucher, 1981), but is not as low as that of *Peucedanum palustre* which had an average of 0.9% (Meredith, 1978).

At Andrew's Wood, the seeds of *L. urens* exhibit two annual emergence pulses, one in summer and the second in autumn (section 4.3.2). Demographic studies of natural populations have shown germination date to have an important influence on seedling survival (Tervis, 1958; Baskin & Baskin, 1972; Gross, 1980). The early emergers often benefit from the full extent of the growing season, have a reasonable establishment rate and reach a large size (Marks &

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Species	Maximum recorded altitude in Britain (m)	Loss in dry weight as % of control	
		Chill	Freeze
Festuca ovina L.	1310	40	36
Poa annua L.	1200	42	77
Festuca rubra L.	1080	28	45
Arrhenatherum elatius Beauv.	550	49	57
Lolium perenne L.	490	26	31
Brachypodium pinnatum Beauv.	380	47	63
Bromus erectus Huds.	310	65	48
Desmazeria rigida L.	300	44	74
Lobelia urens L.	213	39	73
Triticum aestivum L. cv Mercia	*	0	37
Avena sativa L. cv Image	*	26	73
Zea mays L. cv Fiesta	γ	62	**
Oryza sativa L. cv IR 36	ζ	**	**

* Cultivar of North Europe (cold temperature latitudes), γ Cultivar of South Europe (warm temperature latitudes), ζ Cultivar of sub-tropics, ** < 20% survival.

Table 5.6: Growth response of thirteen species to chilling and freezing (Data, except *L. urens*, from Thorpe, Hendry & Duran, 1993).

Prince, 1981; Fenner, 1987). Seedlings of *Lobelia gattingeri* that emerged in late summer were devastated over winter, whilst spring recruits had a good chance of survival (Baskin & Baskin, 1979) and very similar trends were seen for *Bromus tectorum* (Mack & Pyke. 1983). Only one pulse of *Papaver dubium* (Arthur *et al.*, 1973) and *Daucus carota* (Lacey, 1982) seedlings established each year. Similarly, germination timing has a profound effect on the survival of *L. urens* seedlings, with the whole of the autumn cohort lost over winter.

Historically, *L. urens* displayed a preference for seasonally waterlogged soil (section 2.6) and the most dense stands of *L. urens* at Andrew's Wood are confined to the wettest soils (Clements, 1993). Experiments described in this and the previous chapter have shown that sensitivity to soil moisture occurs at both the germination and seedling stage of growth: *L. urens* germinated

well and established better in waterlogged than in moist conditions. The more extensive root system of the waterlogged plants may have been a response to nutrient deficiency caused by the flushing of water through the experimental system. The resultant weights of the two treatments may have been even more different if all the plants had been fed during the experiment. Small seeded species such as *L. urens* are generally confined to wetlands as larger seeds are needed to tolerate drier environments. Schimf (1977) attributed the association between seed size and soil moisture in *Amernthus retroflexus* to the capacity of larger seeds to establish seedlings from deeper soil horizons where moisture is more reliable. However, the mechanisms responsible might be more complex. The characteristics of the rainfall event and the soil conditions may provide selection pressure for larger seed size in dry soil conditions (Leishman & Westoby, 1994a).

Moss featured in all four micro-habitats favourable to survival, although, for reasons outlined in section 4.4, the moss layer of the experimental seed bed did not mimic this effect. This observation offered further support for the dependency of *L. urens* seedlings on soil moisture for successful survival, since a layer of moss reduces rates of moisture loss from the soil (Johnson & Thomas, 1978). Detailed observations show that seedlings situated in bryophyte patches suffered less predation by herbivores than those on bare ground (M. van Dijk, unpublished data cited in During & van Tooren, 1990). Such seedling predation had a pronounced effect on the survival rate of the small-seeded species *Brassica napus* (Bodnaryk & Lamb, 1991).

The effect of depressions on the survival of *L. urens* seedlings was unclear. In the field, depressions featured in only one of the four favourable micro-habitats. In the seed bed, germination only occurred in depressions, removing the opportunity to look at their effect on survival. Although depressions increase the moisture content of soil (Sheldon, 1974; Eldridge *et al.*, 1991), they are associated with soil compaction (Scholefield & Hall, 1985), which reduces pore space, increases soil rigidity and offers a mechanical barrier to radical penetration (Sheldon, 1974).

Cover by higher plants and *Molinia caerulea* litter were impediments to survival as well as emergence of *L. urens*, and litter was absent from the two micro-habitats most favourable to recruitment in the field. Emergence did not occur beneath litter in the seed bed. Hence, survival could not be investigated there. The negative effect of litter on survival may be implemented through reduced soil-to-seed contact (Sydes & Grime, 1981). Litter may act as a mechanical barrier to the extension of newly germinated seedlings because of its weight and density (Al-Mufti *et al.*, 1977; Bosy & Reader, 1995) The small seed reserve means *L. urens* cannot avoid the unfavourable aerial environment below litter through rapid shoot extension (Vasquez & Orozco, 1992; Leishman & Westoby, 1994b).

L. urens, like many plant species (Sagar & Harper, 1961; Putwain & Harper, 1970; Gross, 1984; Weiner, 1982), requires an opening in established vegetation for the successful recruitment of new seedlings. Eighty percent of seedlings surviving to adulthood emerged from micro-habitats without ground cover by higher plants. Golberg & Werner (1983) had significant rank correlations between percentage survival and opening size of *Solidago* spp. and similar results were seen for *Cirsium vulgare* (Silvertown & Smith, 1989). Although the fate of almost 1000 seedlings was followed, the very low survival success of *L. urens* meant there were insufficient data to analyse for correlations between survival and distance to nearest neighbour. Shading explains the negative effect of higher plant cover in part, since shading impaired survival in the seed bed experiment. A previous study of twenty-three species showed small seeded species to be disadvantaged by micro-habitats such as cover by higher plants, where there was a steep gradient of light (Leishman & Westoby, 1994b). Competition for moisture is also likely to contribute to the restriction on establishment beneath plant cover, since waterlogging improved the growth of *L. urens* seedlings. It was surprising, therefore, to see that as many as twenty percent of surviving seedlings emerged from a closed sward (NND = 0). It might be that for such small seedlings, even a gap less than 1 cm offers some solace from competition. Some studies have shown complex interactions of the positive and negative effects of neighbouring individuals on survival. Aguiar *et al.* (1992) indicated how plant cover trapped dispersing seed

and resulted in a larger seed bank below vegetation. Adults also have a positive effect in hostile environments, for example, the marsh elder (*Iva frutescens*) affords aerial protection to seedlings on salt marshes (Bertness & Yeh, 1994).

In summary, the survival of *L. urens* from germination is very low and it is likely to be contributing to controls on the density of British populations. Seedlings that emerge late in the year could not survive the winter. In spring, the recruitment of individuals from seed was improved on wet soil which lacked cover from both higher plants and their litter.

For those individuals which do establish, the duration until first flowering, often termed the juvenile period, is very variable (Hutchings, 1986). Of those individuals followed through 1993-1995, nineteen reached adulthood. Nine of these did so in their first year, i.e. at three to four months old, and ten in their second year. Of the nine plants flowering in their first year, five survived to flower the following year. This is a similar survival rate to that for all flowering individuals (0.60) (section 6.3.1). Hence, with regards to survival, once a plant has flowered, it has truly reached adulthood, even if it does so in its first year.

SIX

Adult autecology

6.1 Introduction

The adult stages of most higher plants encompass the broad phases of growth, reproduction and

post-reproduction (Bazzaz & Ackerly, 1992). The growth rate of an individual is very important

to its population dynamics, since rapid plant growth aids population recovery rates and thus

improves the resilience of populations to sporadic disturbance events (Silvertown, 1982).

Breeding system failure is a common cause of rarity (Weller, 1994). Genetic studies of the

reproductive success of rare species have emphasised inbreeding depression and homozygosity

(Weins *et al.*, 1989). Despite the potential most flowering plant species have for self-

fertilization, diverse mechanisms have evolved to promote out-crossing, presumably to avoid the

loss of fitness that often results from self-fertilization (Weller, 1994). These mechanisms

include the spatial or temporal separation of pollen and stigmas, such as protandity or dioecy.

For example, populations of the buffalo gourd, *Cucurbita foetidissima*, a perennial native to

southwestern America and northern Mexico, contain both female and hermaphrodite plants.

Seeds from females survive their first year almost three times more frequently than seeds from

hermaphrodites, apparently because seeds from hermaphrodites are mostly self-fertilized, which

severely reduces seedling survival (Kohn, 1988). Alternatively, self-mating is prevented through

self-incompatibility. The latter is a blanket term used to cover any selection for cross pollen or

cross-fertilized seed over self (Bateman, 1956; Crowe, 1971; Charlesworth & Charlesworth,

1987; Bertin & Sullivan, 1988; Barrett, 1988). Inbreeding does not dominate breeding system

failure. A self-incompatible species with a specialised pollen vector can become rare as a direct

consequence of the infrequency of pollination events (Bierzychudek, 1981; Weller, 1994). The

seed set of *Lobelia deckenii*, an endemic giant rosette species of Mount Kilimanjaro, Tanzania

is pollinator limited (Burd, 1995). *Dedeckera eurekensis*, a highly heterozygous shrub from the Californian desert, is thought to have lost its reproductive capacity through genetically mediated embryonic abnormalities that lead to development failure and may ultimately result in its extinction (Weins *et al.*, 1989). Faults in a species breeding system can be manifested in many ways (Weller, 1994). Therefore, in this study, a large number of reproductive characters including capsule number, seed number, seed weight and dimensions were measured to explore the full extent of reproductive success of *L. urens*.

In many plant forms, for example, trees and annuals, the post-reproductive phase is clearly marked but in perennials, it can become confused (Harper, 1978). All differentiated cells have restricted lives and undergo senescence. However, meristems are potentially immortal (Salisbury & Ross, 1985). Thus perennial species have the potential for new units to develop juvenile vigour at any time, given favourable conditions, and juvenility, maturity and senescence are reflections of community condition rather than real age (Harper, 1978).

Few long-lived perennials have been subject to demographic study because of the complications of overlapping generations and long life cycles that are without clear structure (Harper, 1977; Bierzychudek, 1982; Ehrlén, 1995). However, a detailed description of a species life history is an essential requirement before the regulating mechanisms which affect populations can be understood (Piñero *et al.*, 1984) and before sensible decisions can be made as to the best form of management, whether designed to restrict or promote a species (Usher, 1972; Given, 1994). Since early studies by Sarukhán on *Ranunculus* (Sarukhán & Harper, 1973; Sarukhán, 1974; Sarukhán and Gadgil, 1974), there have been a handful of successful demographic studies of perennial herbs. These include those of Bierzychudek (1982) who studied *Arisaema triphyllum*, a species whose life history is further complicated by its ability to change sex, and Ehrlén (1995) whose study of *Lathyrus vernus* included the effects of herbivory on the species population dynamics. There have been but a few studies of rare perennials, mostly in North America, the best examples are that of *Isotria medeloides*, one of the rarest orchids endemic to

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eastern North America (Mehrhoff, 1989) and *Panax quinquefolium*, also endemic to North America and threatened by harvesting and habitat destruction (Charron & Gagnon, 1991). Annual data from four years of census (section 3.3.1) have been used in this chapter to investigate the demographic parameters of *L. urens* at Andrew's Wood and Redlake. Statistics of individual growth, longevity and reproductive capacity were analyzed together to show population structure and turnover. In the past, research in plant demography has described populations by determining the relative proportions of individuals of different calender ages (see Harper & White, 1974 for a review). However, it is often impossible to establish the age of herbaceous perennials, except by following them from germination onwards. More importantly, size, reproductive capacity and the plant's role in the community are often not determined by age (Harper, 1977; Gatsuk *et al.*, 1980). It is now recognised that the most appropriate method for understanding the population dynamics of perennial herbs is to focus on size, rather than age, since size is more often strongly correlated with demographic success (Fortanier, 1973; Kawano, 1975; Kawano & Nagai, 1975; Barkham, 1980a, b; Solbrig *et al.*, 1980; Gatsuk *et al.*, 1980; Zhang, 1983; Piñero *et al.*, 1984; Moloney, 1988; Mehrhoff, 1989; see Caswell, 1989 for a review; Charron & Gagnon, 1991; Silva *et al.*, 1991; Åberg, 1992; Ehrlén, 1995).

All plants have evolved in heterogeneous environments under a range of intensities and predictabilities of various abiotic and biotic disturbances, the extremes of which create differing life history strategies (Pavolvic, 1994). At both Redlake and Andrew's Wood, *L. urens* is a member of wet heathland communities that were traditionally maintained by sporadic cattle grazing. For rare plants with specialized adaptations to natural disturbance regimes, variation in the type and scale of disturbance can have significant effects on the population response (Menges, 1991; Hobbs & Huenneke, 1992; Bullock *et al.*, 1994). Since *L. urens* is adapted to a disturbance regime for regeneration from seed (sections 4.4 & 5.4), an assessment of the sensitivity of the adult life stages, especially growth and reproduction, to herbivory and disturbance was undertaken. This assessment was largely field-based but included an analysis of the effects of light quality on both the demography of census plants in the field and on

photosynthetic rate in the laboratory. Although field research on the effects of management on plant demography is preferred (Pavlovic, 1994), photosynthetic light responses are extremely useful in determining species native light environments (Salisbury & Ross, 1985).

6.2 Methods

6.2.1 *Growth and longevity*

Population counts and structure

Annual counts of the flowering spikes of *L. urens* have been carried out for more than a decade at Andrew's Wood and Redlake as described in section 3.1. Monitoring of the flowering individuals within sixteen permanent quadrats at Redlake and Andrew's Wood was undertaken for four years, beginning in 1992. This annual census yielded information regarding the population structure of *L. urens* at the two reserves. The census methods are described in section 3.3.1.

Rhizomal development

Soil was collected from Andrew's Wood, Devon on March 8 1993, spread to a depth of 3 cm over a layer of sand on seed trays and placed in a glasshouse. The glasshouse provided thermostatically controlled minimum heating as a precaution against late frosts and continual watering from below by capillary matting linked to an automatic reservoir. Germination of *L. urens* from the seed bank within this soil began on March 23 1993. Seedlings were pricked out after nine weeks into 2 cm pots filled with 3:1 Levington's peat based and John Innes seed compost and watered as required. On July 12 1993, 250 individuals were planted out into a rotovated plot at 80 cm intervals. Batches of ten were dug up every three months, commencing in November 1993, to observe the development of the rhizome. The number of rosettes were noted and the diameters of the rhizomes were calculated using vernier callipers. An attempt was made to follow the development of the rhizome buds.

6.2.2 *Reproduction*

Fecundity

A fecundity survey was undertaken using a total of 85 plants. In 1993, 50 plants were used, five from each of the ten original permanent quadrats at Andrew's Wood. In 1994, the survey was carried out on all of the flowering plants within the fortnightly census quadrats, representing ten plants from Redlake and 25 from Andrew's Wood. Plants were classified on a binary scale of either young or old. Young individuals were in their first year, ascertained by using plants that were both in a position which had not been occupied by a *L. urens* plant the previous year and seen as a seedling that spring. An old plant was more than one year old and thus had been in a position that had been occupied by a *L. urens* during plant the previous year and had appeared as a rhizome bud that spring. In 1993, an even number of young and old plants were selected. The vegetative morphology of all the plants was quantified as the number of rosettes that a plant possessed and the mean length of the lamina of three rosette leaves, referred to from now on as leaf length. The method of identifying three leaves was to select the first arbitrarily, the second was situated 120° round the stem from this and the third a further 120° around. The mean height of the plant's flowering spikes, the number of branches on a single arbitrarily chosen spike and the mean length of those branches were used to quantify various aspects of the plants reproductive morphology.

Five capsules were harvested from each plant to represent the top, middle and lower part of the main spike and proximal and distal points of a branch. The seeds were collected on ripening, whilst the capsule was still intact and stored in a desiccator. Capsules were opened carefully after drying and the seeds separated from any capsule debris. The number of seeds per capsule was calculated using a Quantimet 570 image analyser. The average of the five counts was also calculated to provide an estimate of the average number of seeds produced per capsule and enumeration of the calyx scars per plant at the end of the season gave an alternative measure of fecundity in terms of capsule production. In 1993, the seed collected was grouped according to maternal origin and seed from the five positions were mixed thoroughly. Ten replicate batches

per plant, each of 100 seeds, were weighed using a Cahn 29 automatic electrobalance to five decimal places. The length, width and depth of ten seeds were measured using a calibrated eye piece graticule on a Kyowa Optic SDL-PL microscope. In 1994, seed from each capsule was divided into two. Half the seed from each plant was used, as in 1993, to observe the variation in seed size with maternal morphology, for example the number of rosettes or the spike height. The remaining half was classed across all plants within each reserve according to the position on the spike (bottom, middle, top, proximal and distal). This yielded data on the variation in seed size with its position on the flowering spike.

Flowering phenology

The timing of the emergence of the first flowering spike and the opening of the first flower of each plant was recorded at Andrew's Wood in 1994 as part of the fortnightly census (section 3.3.2).

Pollination

The stamens and style of *L. urens* are fused, which dismissed the use of emasculation to prevent self-pollination, and thus prevented the observation of purely outcrossed plants and of all combinations (manually outcrossed, manually self-fertilized and open) on a single individual. Investigations were carried out on the seed set of manually outcrossed, manually self-fertilized and isolated individuals. Seed was sown in March across the surface of 24 cell seed tray inserts filled with a ratio of John Innes Seed to Levington's Multipurpose compost and incubated in a glasshouse. The glasshouse provided thermostatically controlled minimum heating as a precaution against late frosts and continual watering from below by capillary matting linked to an automatic reservoir. Germination commenced after two weeks and seedlings were thinned at intervals to leave one individual per cell. Thirteen weeks after germination, on formation of a root ball, sixty seedlings were transferred to 6 cm pots containing 4:1 Levington's to John Innes Number 2 compost. The experiment commenced on June 14 1993. The 20 manually outcrossed plants remained in the glasshouse. Material that prevented the passage of 15 µm

pollen grains between plants but offered no obstruction to water vapour and light could not be obtained. Hence, the 20 manually self-fertilized and 20 isolated plants were separated by placing one per room on the west-facing sills of an eight-storey university building. Paint brushes were used to move pollen from newly dehisced anthers to receptive stigmas twice weekly for both manual regimes. Isolated plants were left untouched, with insect interaction being prevented by swathing in horticultural fleece. The fleece reduced light levels to 58% of ambient and, therefore, its effect was investigated on five manually crossed plants versus five controls in the glasshouse. All plants were positioned to obtain maximum available light and stood in 10 mm of water which was replenished every other day. The experiment ran until October 28 1993.

Five capsules were harvested per plant from arbitrarily chosen points at the top, middle and lower part of the main spike and at proximal and distal points on a branch. These were collected in vials as the individual capsules dried and showed transparency but whilst they were still intact. Vials were stored with the lids removed in a desiccator to ensure that the seeds were dry. Capsules were opened carefully after drying and the seeds separated from any capsule debris. The number of seeds per capsule was calculated using a Quantimet 570 image analyser. Seeds were then classed together according to their treatment: crossed, selfed and isolated, and mixed thoroughly. Ten batches of 100 seeds, from each of the three treatments were weighed using a Cahn 29 automatic electrobalance to five decimal places. The length, width and depth of thirty seeds from each treatment were measured using a calibrated eye piece graticule on a Kyowa Optic SDL-PL microscope. Counts of the number of calyx scars at the end of the experiment enabled an estimation of the total seed production per plant under each regime.

The viability of the seed was tested under the 29:15°C alternation (14:10 hour thermo- and photoperiod) following the procedure outlined in section 4.2.1. This regime was chosen, since it had been found to optimize percentage germination in section 4.3.1.

6.2.3 *The effects of environmental variation on adult demography*

The effects of herbivores

The effect of herbivores on the demography of plants at Andrew's Wood was observed as part of the annual census (section 3.3.1). However, over the census period, there was no control over grazing intensity. The reserve was grazed over the autumn-winter period and the intensity varied from four animals from October to December in 1993, to 13 animals for two weeks in October 1994. A manipulative field experiment was performed to observe the effect of defoliation intensity, as *in situ* research continues to be a good place for understanding the relationship between management and species life history (Pavlovic, 1994). On May 8 1995 a 5 m² plot was marked out at Andrew's Wood with wooden stakes. Thirty-six plants, of two size classes (one rosette = small, and three to twelve = large plants), were subjected to three different treatments. The treatments were:

(i) unclipped (control),

(ii) clipped to leave 20 mm of lamina and

(iii) clipped to leave 10 mm of lamina.

The effect of treatment on plant size, number of rosettes, mean leaf length and mean spike height of the plants were recorded on 18 July 1995.

The effects of the light environment

(i) Experimental

Seed taken from the pool collected in autumn 1993, as described in section 4.2.1, was sown on May 3 1994 in 40 compartment seed trays filled with sterilised soil from Andrew's Wood and germinated in an unheated glasshouse. The soil was kept moist. Following germination, seedlings were thinned to one individual per compartment. Ten weeks after germination, on formation of a root ball, twenty seedlings were transferred to 6 cm pots containing 4:1 Levington's to John Innes Number 2. At 17 weeks old, when plants were in full flower, the photosynthetic rate of ten individuals at a range of light intensities was measured using an Infra-Red Gas Analyser (IRGA, Analytical Development Company, Series 225) with an open air

circuit. Roots were washed, plants stood in conical flasks filled with water, and stems supported by cotton wool at the flask neck. Light was provided by a 6 kW xenon arc lamp, giving a maximum photon flux density (PFD) of about 665 μM m^{-2} s^{-1} at the foliage surface (although, because of the vertical gradient of PFD, PFD was not the same on every leaf). The PFDs of 1.2, 9.9, 19.4, 76.0, 156.0, 290.0, and 487 μM m^{-2} s^{-1} were provided by screens with differing numbers of layers of butter muslin. Afterwards, leaf areas were measured with a LI-3000 area meter.

(ii) Field

The ratio of red to far-red light gives an index of the degree of canopy shade (section 2.3.3). This was measured, along with vegetation height, as part of the fortnightly census (section 3.3.2). Readings were taken at 50 cm intervals along the border of each quadrat and the average of the 10 readings per quadrat calculated to show variation between grazing treatments, compartments, sites and years.

6.3 Results

6.3.1 Growth and Longevity

Population counts

Between 1975 and 1995, there were large fluctuations in the size of the *L. urens* populations of both Andrew's Wood and Redlake (Figure 6.1a). There was no correlation between the counts of flowering spikes at the two reserves, nor between counts of the compartments within Andrew's Wood (Table 6.1). The number of spikes in compartment D shows wide fluctuations, for example, rising from 187 plants to 3822 in two years (Figure 6.1b). The number of spikes in compartment C gradually declined from 1976 until 1992, when scalloping, or cutting of the compartment's woodland boundaries to enlarge the transition, was introduced (Figure 6.1b). In compartment A8, the number of spikes has increased since a dramatic decline in numbers in 1986 (Figure 6.1b). There was a significant correlation between the number of flowering spikes

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in C and A8 between 1975 and 1995 but this was negative which made no sense (Table 6.1).

	Redlake	D	C
Andrew's Wood	-0.45		
C		-0.20	
A8		0.38	-0.67**

** $P < 0.01$.

Table 6.1: Spearman rank correlation coefficients between the counts of flowering spikes at Redlake and Andrew's Wood and within the three grassland compartments of Andrew's Wood (D, C, and A8). The data were collected for the majority of years between 1975 and 1995 and analyzed using pair-wise deletions.

The consistently smaller population size at Redlake over the past twenty years (Figure 6.1a) could partly be attributed to the smaller area under grassland at the reserve: 2.81 hectares compared to 4.42 ha at Andrew's Wood's. Data from the annual census of plants within permanent quadrats showed no significant difference in the number of plants per m^2 between the four years of census data ($P > 0.05$, Table 6.2). However, there was a significant difference in plant density among the sites/compartments ($P<0.001$, Table 6.2).

	d.f.	MS	F
Years	3	13.67	0.40
Sites/compartments	6	110.01	11.01***

*** $P < 0.001$

Table 6.2: Results of two one-way ANOVAs of number of flowering plants per square metre of census quadrats. Degrees of freedom (d.f), mean squares (M.S) and F-ratios are indicated.

Focusing on 1995, the quadrats of Redlake had significantly less plants per m^2 than compartments A8 and D of Andrew's Wood (Figure 6.2). Within Andrew's Wood there was a significant difference in plant density between compartments and grazing treatments: compartment C had a lower density than compartment A8 and the grazed areas of compartment D which in turn had fewer plants that the ungrazed quadrats of compartment D (Figure 6.2).

(a) Totals for Redlake & Andrew's Wood

(b) Compartments within Andrew's Wood
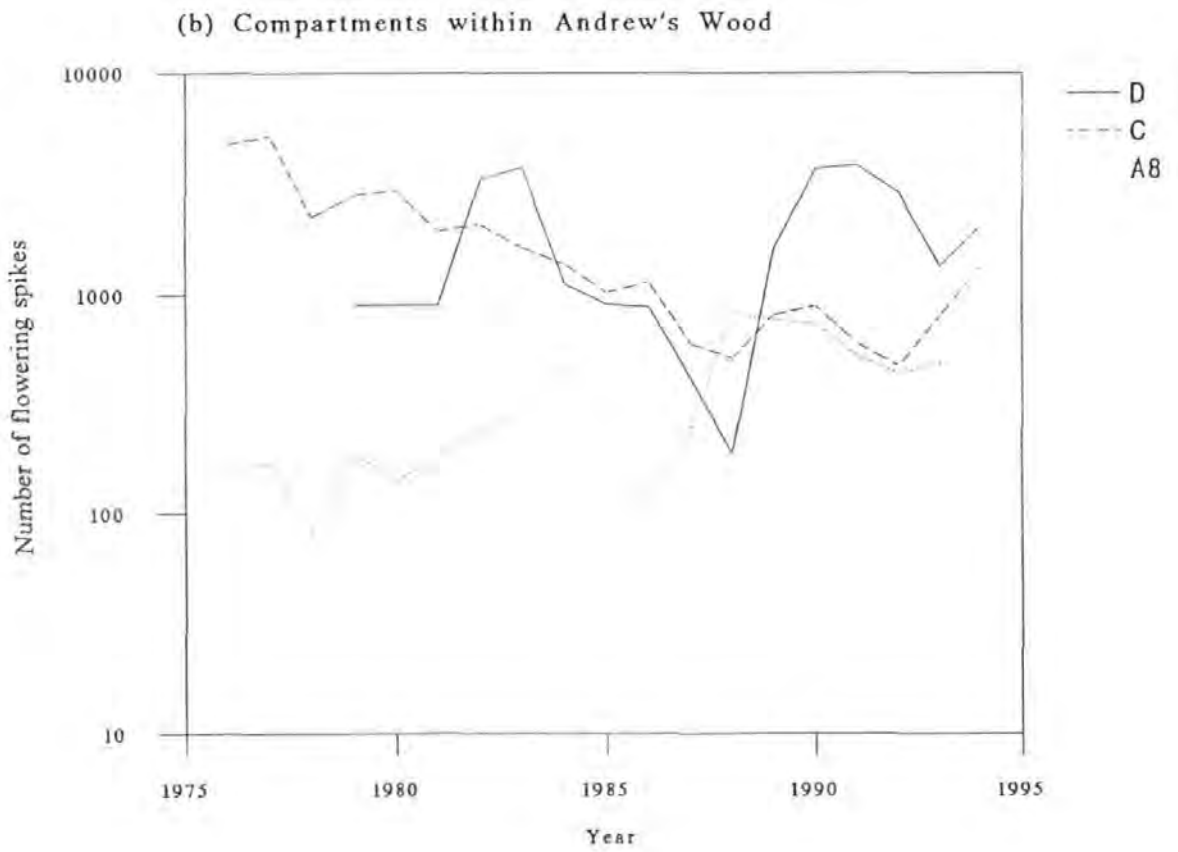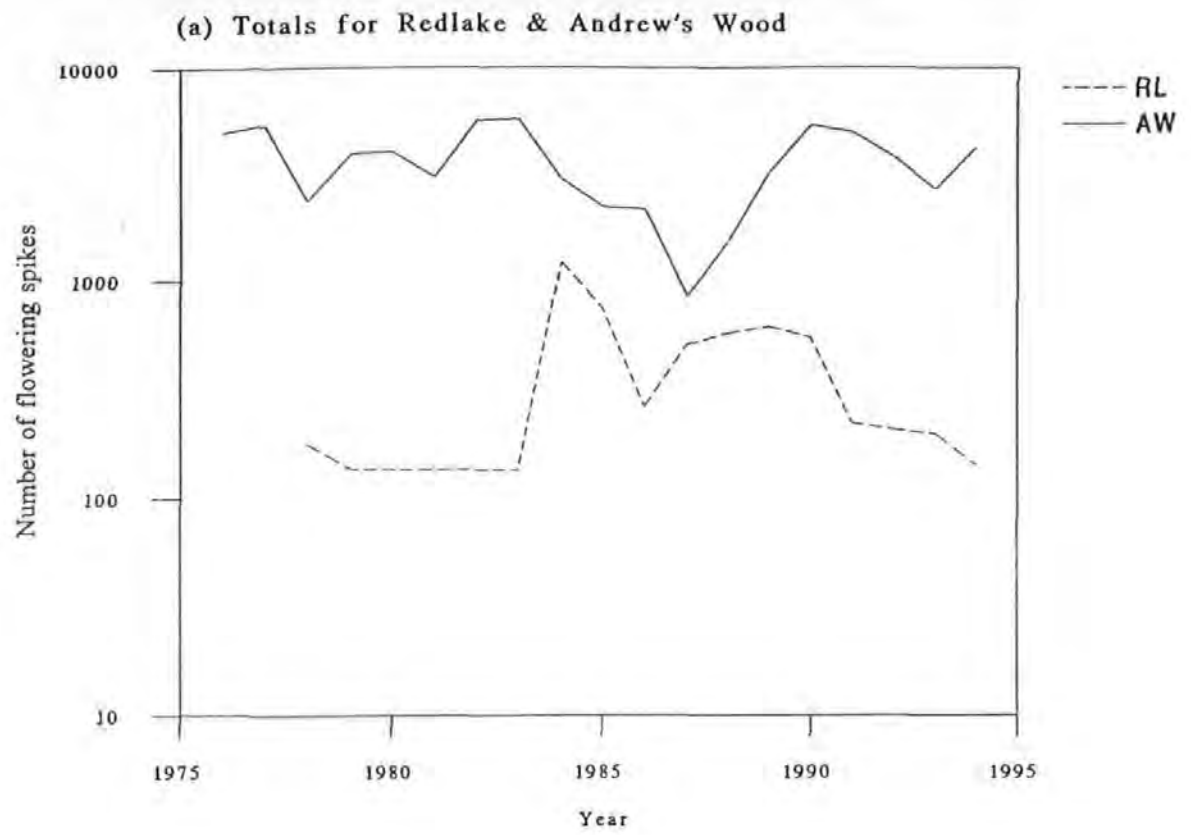
Figure 6.1: Annual counts of the flowering spikes of *L. urens*.
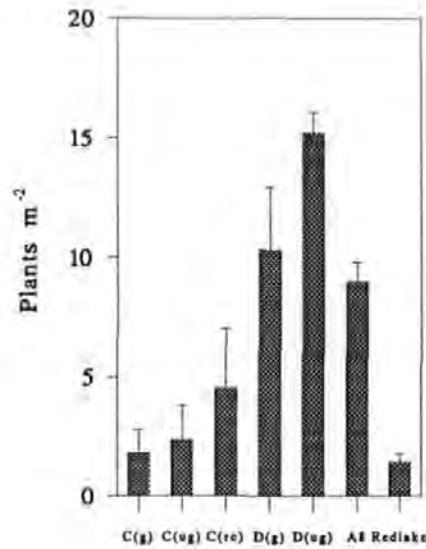
Figure 6.2: Number of flowering plants per square metre of census quadrats at Redlake and within Andrew's Wood in compartments D and C (grazed (g), ungrazed (ug) and recently cleared (rc) quadrats) and compartment A8, 1995. Bars show one standard error of the mean.

Population structure

Emergence was low and the death rate high in compartment C, which indicated that the sub-population in this compartment was in decline; all plants in the ungrazed quadrats had died by 1995 (Figure 6.3). Redlake also had very little emergence, but a lower death rate meant the population was more stable (Figure 6.3). The proportion of deaths was consistently lower in the ungrazed quadrats than the grazed areas of compartment D but over the four years of census, emergence in the ungrazed quadrats fell from twenty percent to virtually zero (Figure 6.3). Emergence in A8 was always high but the death rate decreased over the census period (Figure 6.3) resulting in population growth. The recently cleared areas of compartment C showed the pattern of turnover characteristic of recent colonisation following disturbance, that is new emergence followed by a high death rate before the population stabilizes (Figure 6.3). Overall, the turnover at Redlake was much lower than Andrew's Wood: 86% of flowering plants present at end of study were there at the beginning at Redlake compared to only 35% at Andrew's Wood. Within Andrew's Wood, ungrazed compartment D had a much lower turnover, 65%,
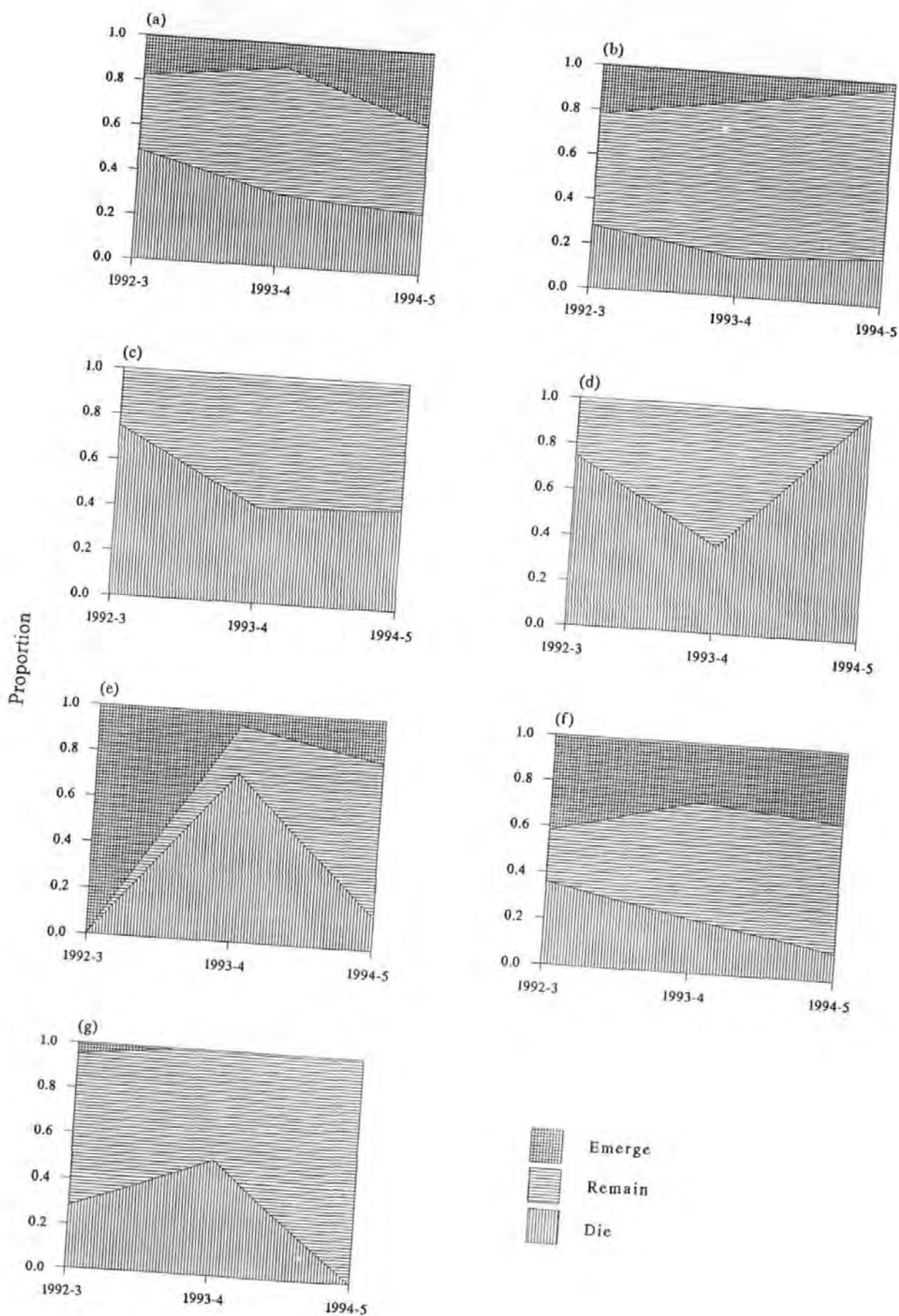
Figure 6.3: Annual census data 1992-1995 showing the proportion of *L. urens* plants that died, remained or emerged within (a) grazed compartment D, (b) ungrazed compartment D, (c) grazed compartment C , (d) ungrazed compartment C, (e) recently cleared compartment C, (f) compartment A8, (g) Redlake.

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than the grazed compartment D 29%. On average, over both reserves, an established plant had a 63% chance of survival to the following year. There was no evidence of established plants "missing" years by not producing above ground structures or flowers for one year and then returning.

Kruskal-Wallis tests were applied to data on the number of rosettes per plant grouped into the seven compartments/grazing treatments: Redlake, Andrew's Wood compartments D (grazed, ungrazed), C (grazed, ungrazed and recently cleared) and A8 across the years 1992-1995. Analyses for differences between site/grazing treatments at the initiation of the study and for significant changes in the number of rosettes within each site/grazing treatment, over the four years of the study, were undertaken. Initially in 1992, there was a significant difference in the rosette number per plant between sites (Kruskal-Wallis test statistic = 27.36, $P<0.001$). All compartments/grazing treatments in 1992 had a median rosette number of one, except A8, which had a median of two. Over the duration of the study, there was no significant change in the median number of rosettes per plant in the orginal areas of compartment C ($P>0.05$, Table 6.3). However, the other compartments/treatments showed significant differences in rosette number between years (Table 6.3). In the ungrazed quadrats of compartment D, the recently cleared area of compartment C and at Redlake, the median number of rosettes per plant increased steadily over the four years (Table 6.3), whilst the median rosette number per plant decreased in A8 (Table 6.3). Although there was a significant difference in the number of rosettes per plant in the grazed area of compartment D, this was not consistent with time since treatment began ($P<0.001$, Table 6.3).

An increase in the median rosette number of a population may be a manifestation of a rapid adult growth rate or a paucity of emergence (decreasing the number of plants with few rosettes), whilst, in contrast, a decrease in the median can result from the loss of large plants or from a high emergence. To investigate the meaning of the changes seen in the quadrats over the four years, it was necessary to look at rosette number frequency distribution curves. Figure 6.4

shows that the changes in median rosette number of plants in A8 and Redlake resulted from a change in the number of plants with only one rosette, whilst the frequency of large plants stayed the same (Figure 6.4a & b). The higher median rosette number in 1994 from plants of the grazed areas of compartment D (Table 6.3) was the result of there being fewer plants with one or two rosettes that year (Figure 6.4c). The increase in the median rosette number of plants in the ungrazed quadrats of compartment D was a product of both a decrease in the number of plants with one or two rosettes and an increase in the number of plants with more than three rosettes (Figure 6.4d).

Year	Redlake	C(g)	C(ug)	C(rc)	A8	D(g)	D(ug)
1992	1	1	1	-	2	1	1
1993	1	2.5	2	1	1	1	2
1994	2	2	2	3	1	2	3
1995	2	1	-	3	1	1	3
test stat.	10.01*	4.55	4.66	8.24**	14.60**	23.30**	140.71***

** $P<0.01$, *** $P<0.001$

Table 6.3 Kruskal-Wallis test of change in median number of rosettes per plant over the four year census period at Redlake and within Andrew's Wood in compartments D and C (grazed (g), ungrazed (ug) and recently cleared (rc) quadrats) and compartment A8, 1995.

In contrast to rosette number, there was no consistency in spike height across compartments or grazing treatments (Table 6.4). Plant from grazed quadrats did not have shorter or longer spikes than those from ungrazed areas. Although the ANOVAs among years were highly significant, the mean spike height of each compartment/grazing treatment showed no constant trends among years (Table 6.4). Phenological assynchrony in spike height was demonstrated. For example, in July, when annual censuses were carried out, the spikes of plants in A8 were higher in 1993 than 1994 (Figure 6.5). However, in August of 1994, the spikes in A8 surpassed any height reached in 1993 (Figure 6.5). The situation in July did not reflect that of the full year because

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of climatic variations between the two years. Perhaps favourable weather early in 1993 promoted an early peak in spike height or, alternatively, a longer growing season in 1994 permitted continued spike growth. Annual maximum spike height could be a useful measure of plant size. However, identification of a maximum height would require a number of censuses rather than one annual census.
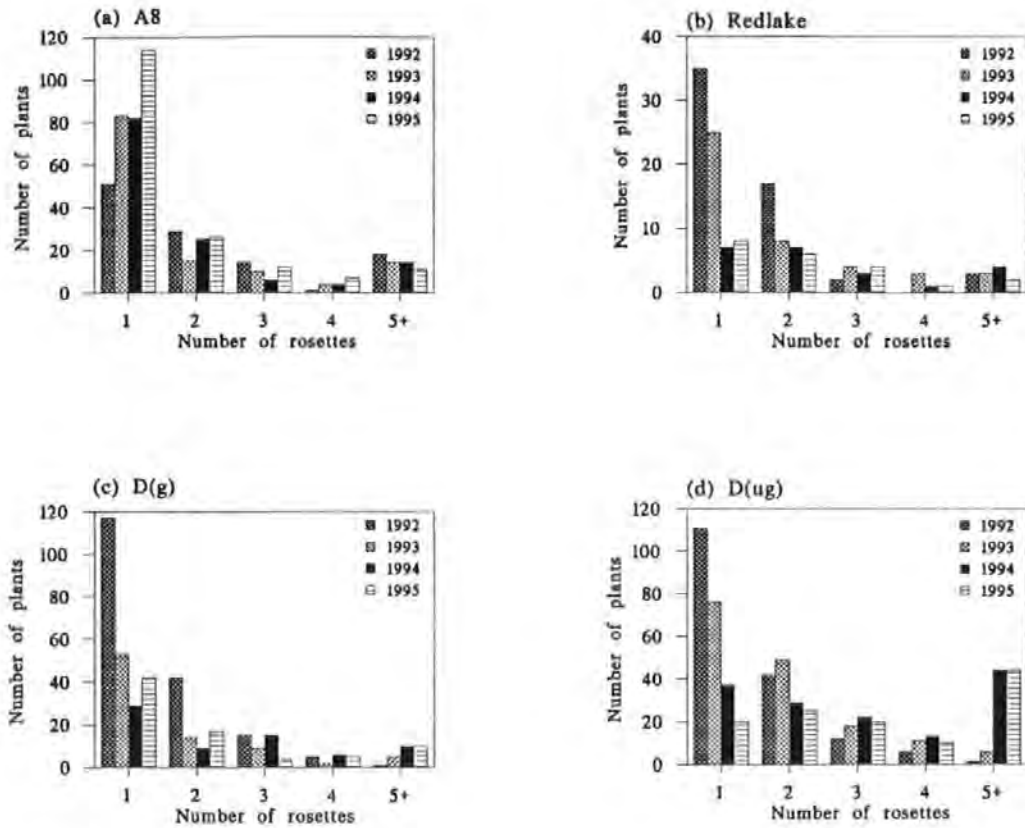
Figure 6.4: Number of rosettes per plant censused between 1992-1995 in (a) compartment A8 of Andrew's Wood, (b) Redlake, (c) grazed areas of compartment D, Andrew's Wood and (d) ungrazed areas of compartment D, Andrew's Wood.

Overall, there was an association between possessing more than one rosette and increased survival chances across Redlake and Andrew's Wood (Table 6.5). Individual analyses showed this association occurred in compartment A8 and the ungrazed quadrats of compartment D but there was no sensible relationship between rosette number and survival in the grazed areas of compartment D (Table 6.5). The number of plants in compartment C and Redlake were too low to perform individual analyses.

	Means of compartments and sites						
Date	Redlake	C(g)	C(ug)	C(rc)	D(g)	D(ug)	A8
1992	64.55	30.63	36.15	-	36.66	43.97	47.75
1993	68.15	25.84	40.59	42.25	30.67	63.75	41.89
1994	44.53	36.04	41.33	51.68	35.22	60.23	43.26
1995	53.48	36.00	-	52.44	44.35	61.51	39.21
d.f.	3	3	2	2	3	3	3
MS	9286.47	554.57	223.13	2041.85	3250.79	21620.74	3070.00
F	57.26***	5.84***	0.84	9.59***	16.76***	102.73***	10.33***

*** $P < 0.001$

Table 6.4: Results of seven one-way ANOVAs of change in spike height over four year census period at Redlake and within Andrew's Wood in compartments D and C (grazed (g), ungrazed (ug) and recently cleared (rc) quadrats) and compartment A8. Degrees of freedom (d.f), mean squares (MS) and F-ratios are indicated.
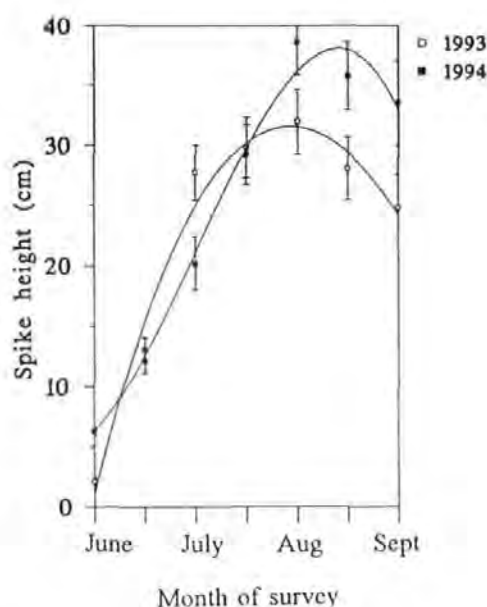
Figure 6.5: Temporal variation in spike height in compartment A8 of Andrew's Wood 1993 and 1994. Bars show one standard error either side of the mean. Equations for fitted curves are: 1993 $y = 0.07x^3 - 2.81x^2 + 22.00x - 18.46$, $r^2 = 0.97$ and 1994 $y = -0.39x^3 + 3.52x^2 + 1.69x + 4.92$, $r^2 = 0.99$.

Rosette number	Total of Andrew's Wood and Redlake		A8	
	Survive	Die	Survive	Die
1	401 (454)	359 (306)	125 (134)	98 (89)
2	216 (206)	129 (139)	47(40)	20 (27)
3	104 (94)	54 (64)	18 (18)	12 (12)
4+	167 (133)	56 (90)	37 (35)	21(12)
χ^2		107.85***		56.78***

	D(g)		D(ug)	
	Survive	Die	Survive	Die
1	74 (75)	75 (74)	136 (168)	91 (59)
2	32 (40)	48 (40)	104 (93)	21 (32)
3	25 (22)	18 (21)	48 (43)	10 (15)
4+	22 (16)	10 (18)	80 (64)	7 (23)
χ^2		12.74**		37.45***

** $P < 0.01$, *** $P < 0.001$

Table 6.5: Chi-square tests for association between number of rosettes across both Andrew's Wood and Redlake and within Andrew's Wood in compartment D (grazed (g), ungrazed (ug) quadrats) and compartment A8 and survival to following census. Observed (expected) values, 3 degrees of freedom.

There was also an association between the change in rosette number and survival across Redlake and Andrew's Wood: plants with an increasing number of rosettes and those with a fluctuating rosette number were more likely to survive than expected (Table 6.6). Again, this relationship occurred in the ungrazed quadrats of compartment D but was less clear (and less significant this time) in the grazed areas of compartment D (Table 6.6). The number of plants in compartments C and A8 and at Redlake were too low to perform individual analyses.

Change in rosette number	Total of Andrew's Wood and Redlake	
	Survive	Die
<	115 (110)	45 (50)
>	33 (44)	31 (20)
−	74 (84)	49 (39)
~	80 (64)	13 (29)
χ^2		35.84***

	D(g)		D(ug)	
	Survive	Die	Survive	Die
<	14 (12)	11 (13)	63 (17)	11 (57)
>	6 (9)	12 (9)	8 (14)	10 (4)
−	7 (9)	10 (9)	18 (23)	11 (6)
~	16 (12)	7 (11)	29 (24)	2 (7)
χ^2		8.14*		37.16***

* $P < 0.05$, *** $P < 0.001$

Table 6.6: Chi-square tests for association between change in the number of rosettes across both Andrew's Wood and Redlake and within Andrew's Wood in compartment D (grazed (g), ungrazed (ug) quadrats) and survival to following census. Observed (expected) values, 3 degrees of freedom (< increasing, > decreasing, − static, and ~ fluctuating rosette number).

Rhizomal development

There was no relationship between position of a bud on the rhizome and its propensity to develop into a root or a shoot. Roots and shoots were inter-dispersed on the rhizome (Plates 6.1 & 6.2). Rhizome morphology can be estimated from the plants age or vegetative size in a number of perennial species (Silvertown, 1982; Sutherland & Walton, 1990). A Kruskal-Wallis test was applied to look for variation among the diameters of *L. urens* rhizomes over three monthly intervals from November 1993 to November 1994. The diameters of the rhizomes decreased slightly during the year of measurement although this difference was not significant (Kruskal-Wallis test statistic = 6.11, $P > 0.05$, Figure 6.6). The reason for this decline in median size was that the rhizomes of a number of plants divided to form up to five clonal individuals in the autumn of their second year (Figure 6.6 & Plate 6.2), each of which was measured

Plate 6.1: Rhizome of a six month old *L. urens* plant, November 1993. Note that new rosettes for the following year are already formed and that these can emerge from the rhizome below the roots.

Plate 6.2: The rhizome of an eighteen month old *L. urens* plant, November 1994, showing division into two individual plants.

separately. There was no correlation between the number of clonal individuals the parent divided into (ramets) and the number of rosettes per gamet (Spearman's rank correlation coefficient = -0.58, $P>0.05$). It had been planned to continue observation of the rhizomes of these plants for a further year. However, too few survived the second winter to continue the investigation. The cause of death was unknown.
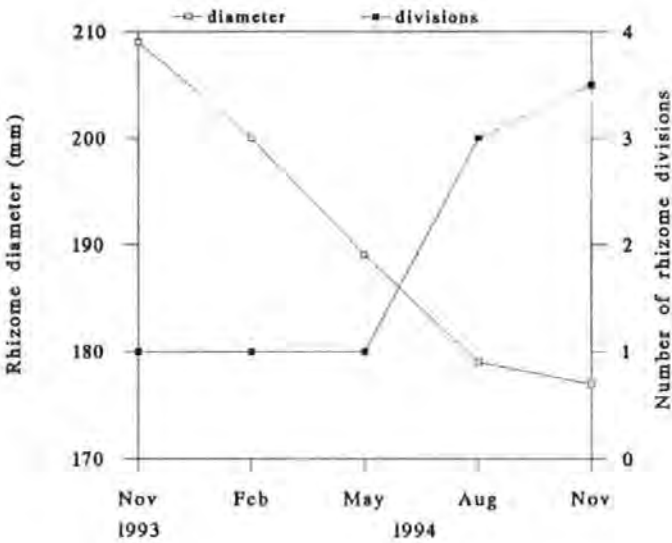
Figure 6.6: Rhizomal development in terms of median diameter and mean number of divisions measured from garden plants dug up at three monthly intervals.

6.3.2 Reproduction

Fecundity

Full data sets were obtained for 61 plants, from Andrew's Wood, 35 in 1993 and nineteen in 1994, and from Redlake, seven in 1994. The spikes of the remaining plants were separated from the rosette by wind, rain or trampling before all the data had been collected. Using the combined data collected in 1993 and 1994 from both Andrew's Wood and Redlake, on an individual inflorescence, there was no correlation between the number of capsules per plant and the mean number of seeds per capsule or the size of the seeds within the capsules. Neither was the number of seeds per capsule correlated with their size (Table 6.7). Significant correlations

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only existed between seed weight and width and between length and depth. The number of capsules on a spike, the number of seeds per capsule, the weight and the length of individual seeds all gave separate measures (Table 6.7). Hence, these four characters were used to investigate variation in fecundity .

	No. of capsules/ plant	Ave.seeds/ capsule	Seed weight	Seed length	Seed depth	Seed width
Ave. seeds/capsule	0.31					
Seed weight	0.05	-0.02				
Seed length	0.33	0.00	0.32			
Seed depth	0.21	0.17	0.13	0.43*		
Seed width	0.04	-0.24	0.45*	0.27	-0.15	
Means	34	142	18.30µg	501.96µm	296.15µm	193.08µm

* $P < 0.05$.

Table 6.7: Spearman rank correlation coefficients for five measures of the fecundity of *L. urens* applied to combined data collected from Andrew's Wood in 1993 and 1994, and from Redlake in 1994.

There was no significant difference in fecundity between 1993 and 1994 or between Andrew's Wood and Redlake, when measured in terms of the number of capsules per plant or the length and weight of seeds. However, plants in 1993 at Andrew's Wood produced significantly more seeds per capsule than those from either Andrew's Wood or Redlake in 1994 (Table 6.8). With so few replicates, the variation in fecundity between compartments of Andrew's Wood could not be investigated.

	Test stat.
No. of Capsules	0.56
Average seeds/capsule	14.45***
Seed weight	1.30
Seed length	0.22

*** $P < 0.001$

Table 6.8: Kruskal-Wallis test statistics for differences in *L. urens* fecundity between Andrew's Wood in 1993 and 1994, and from Redlake in 1994.

There was a developmental hierarchy at both Andrew's Wood and Redlake in 1993-4 with the terminal capsules containing significantly fewer seeds (Figure 6.7). However, seed collected from Andrew's Wood in 1994 from the terminal capsules (top and distal) were significantly lighter (Kruskal-Wallis test statistic = 20.99, $P<0.001$) and shorter (Kruskal-Wallis test statistic = 100.02, $P<0.001$) than those from lower down the spike, whereas seed collected from Redlake in the same year from top and distal capsules were heavier (Kruskal-Wallis test statistic = 14.30, $P<0.001$) and longer (Kruskal-Wallis test statistic = 28.73, $P<0.001$) than those from lower down the spike (Figure 6.8).
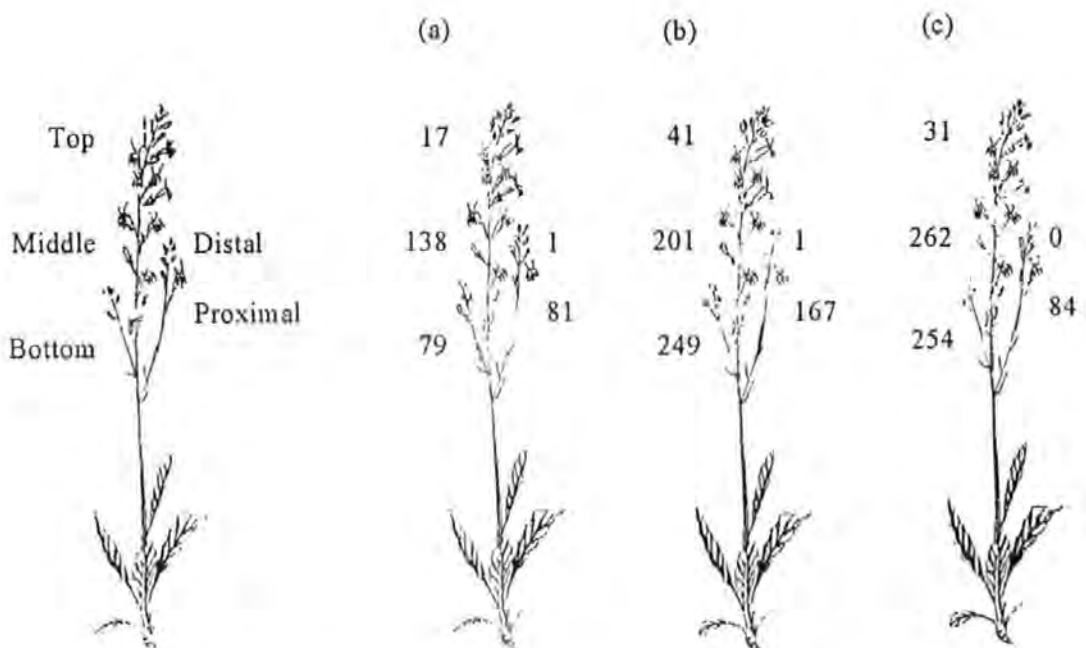
Figure 6.7: Median seed number per capsule classed according to position on flowering spike (a) Andrew's Wood, 1993, (b) Andrew's Wood, 1994, and (c) Redlake 1994.

Of the six morphological characteristics measured as part of the fecundity census, branch number was strongly correlated with branch height, spike height and leaf length across both years and sites (Table 6.9). Hence, these three characters could be discarded from further analyses, with branch number taken to be representative of all of them. Branch height and leaf length were discarded. However, spike height was retained, since it was the only measure of inflorescence size recorded in the annual census and its association with fecundity was of interest in the matrix analysis (section 8.2.1). Leaf number was retained in analyses as an

independent measure of plant size (Table 6.9). Rosette number was also retained, although it was correlated with other characters at Redlake, since these correlations were only marginally significant and were not consistent with results from Andrew's Wood (Table 6.9).
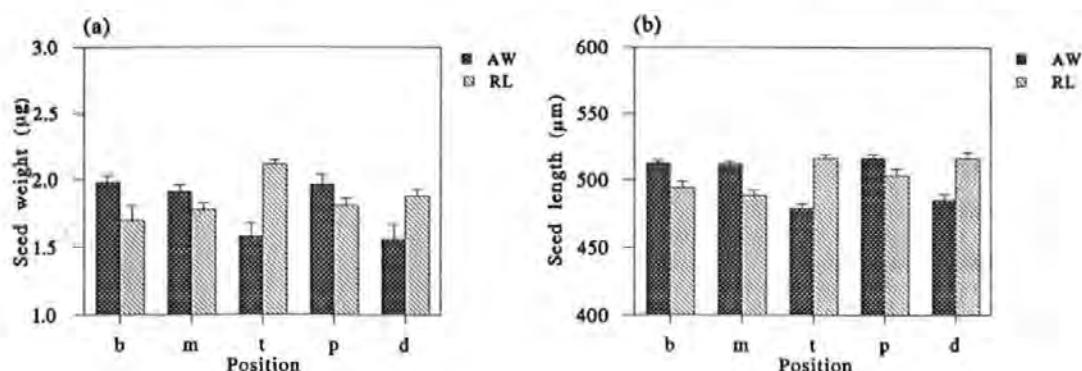
Figure 6.8: Variation in (a) seed weight and (b) length with position on flowering spike (b = bottom of main spike, m = middle of main spike, t = top of main spike, p = proximal position on branch, d = distal position on branch) for Andrew's Wood (AW) and Redlake (RL), 1994. Bars show one standard error above the mean.

		Rosette number	Leaf number	Leaf length	Spike height	Branch number
Leaf number	AW93	-				
	AW94	0.26				
	RL94	-0.77*				
Leaf length	AW93	0.15	-			
	AW94	0.10	0.15			
	RL94	0.46	0.59			
Spike height	AW93	0.12	-	0.64***		
	AW94	0.32	0.01	0.72**		
	RL94	-0.78*	0.54	0.24		
Branch number	AW93	0.13	-	0.63***	0.66***	
	AW94	0.23	0.35	0.35*	0.63**	
	RL94	-0.44	0.60	0.80*	0.77*	
Branch height	AW93	0.23	-	0.69***	0.64**	0.85***
	AW94	0.35	0.03	0.29	0.64**	0.76***
	RL94	-0.70*	0.61	0.25	0.78*	0.80*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 6.9: Spearman rank correlation coefficients for six measures of the morphology of *L. urens* applied to data from Andrew's Wood, 1993 (AW93), and 1994 (AW94) and from Redlake, 1994 (RL94).

The vegetative size (rosette number, leaf number) of *L. urens* was not correlated with the number of capsules, the number of seeds nor the weight of the seeds the plant produced. There were significant correlations between fecundity and plant morphology at Andrew's Wood and Redlake but these were not consistent across the two sites. At Andrew's Wood, a taller, more branched spike produced both more capsules and more seeds in those capsules for both years, whereas, at Redlake in 1994, inflorescence size was not related to capsule or seed number (Table 6.10). Seed length was the only measure of fecundity to be significantly correlated with plant morphology at Redlake, but seed length was not correlated with plant morphology at Andrew's Wood (Table 6.10). Seed weight was not correlated with plant morphology at either Andrew's Wood or Redlake in 1994.

Plants in their first year were no less fecund than older plants (Table 6.11). However, age may be a weak predictor of seed length, since, that year's seedlings tended to produce fewer rosettes than well established plants (Table 6.11).

		Rosette number	Leaf number	Spike height	Branch number
Number of capsules	AW93	-0.23	-	0.36*	0.51**
	AW94	0.40	0.24	0.73*	0.80***
	RL94	-0.69	0.94	0.59	0.55
Average seeds/capsule	AW93	0.33	-	0.33	0.42*
	AW94	0.12	-0.01	0.38	0.59**
	RL94	-0.54	0.35	0.05	0.48
Seed weight	AW94	-0.05	-0.13	-0.01	-0.04
	RL94	0.17	0.04	-0.10	-0.15
Seed length	AW94	0.03	0.03	-1.21***	0.01
	RL94	-0.45***	0.51***	0.37***	0.14***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 6.10: Spearman rank correlation coefficients for four measurements of the morphology of *L. urens* plants against four measurements of fecundity at Andrew's Wood, 1993 and 1994 and Redlake, 1994.

	Z
No. of capsules	-0.48
Ave. seeds/capsule	-0.30
Rosette number	-2.15*
Leaf number	-1.91
Leaf length	-0.54
Spike height	1.33
Branch number	1.58

*P < 0.05

Table 6.11: Two sample comparison, Mann-Whitney U test statistics (Z) showing differences in two measures of fecundity and five measures of plant morphology between old and young individuals at Andrew's Wood, 1993 and 1994, and Redlake, 1994.

Flowering phenology

At Andrew's Wood in 1994, *L. urens* began to extend flowering spikes on May 16 and the first flower opened on July 11. Of the 34 census plants which flowered that year, all (100%) extended spikes in May and twenty-six (76%) began flowering in the month of July. There was no significant correlation between the timing of either spike extension or flowering and plant size (Table 6.12).

	Rosette number	Leaf length	Spike height
Time of spike extension	0.08	-0.13	-
Time of first flowering	-0.04	-0.20	-0.30

Table 6.12: Spearman rank correlation coefficients of time of spike extension and first flowering with size at that time for plants at Andrew's Wood, 1994. $P>0.05$.

Pollination

L. urens can self-pollinate successfully. There was no significant difference in the fecundity of plants swathed in fleece compare to controls (Mann-Whitney U, test statistic $Z = 0.58$, $P>0.05$ for seed numbers per capsule and 0.53, $P>0.05$ for capsule numbers per plant). A similar number of capsules per plant (Table 6.13) verified that plants of the three treatments had been kept under equivalent conditions. The number of seeds per capsule was significantly lower for

isolated plants than for those which had been fertilized manually (median seeds per capsule, crossed (C) = 33, selfed (S) = 20, isolated (I) = 0) (Kruskal-Wallis test statistic = 42.16, $P<0.001$) but there was no significant difference between crossed and self-fertilized plants (Kruskal-Wallis test statistic = 0.84, $P>0.05$). There was very little difference in the number of capsules or in the seed dimensions of self-fertilized, crossed or isolated plants (Table 6.13). Seed which had been cross-fertilized was shorter, deeper and wider than selfed and isolated seed (Figure 6.9a) and, although these differences were not significant (Table 6.13), as a result, crossed seed was significantly heavier than selfed and isolated seed (Table 6.13 & Figure 6.9b). This difference in weight did not affect seed viability, which was not different between treatments (Figure 6.10).

	MS	F
No. of capsules	3743.54	0.12
Seed weight	0.17	8.95***
Seed length	2661.90	3.00
Seed depth	667.00	1.09
Seed width	3133.96	2.35

*** $P<0.001$

Table 6.13: Five one-way ANOVAs, each with two degrees of freedom, showing difference in fecundity between crossed, selfed and isolated plants of *L. urens*. Mean squares (MS) and F-ratios are indicated.

(a)

(b)
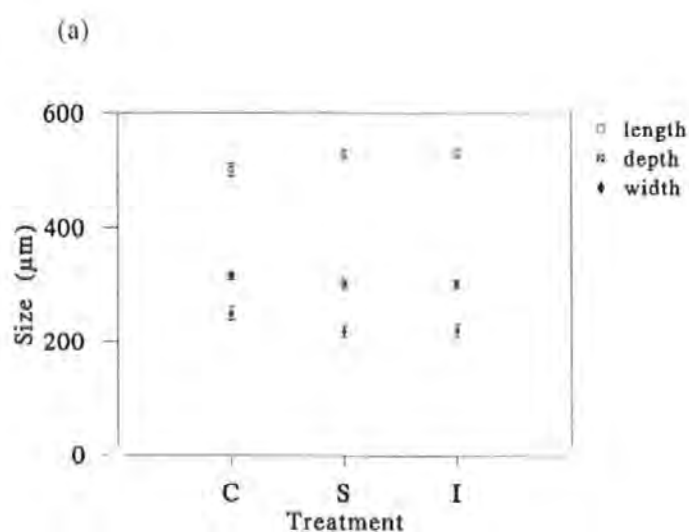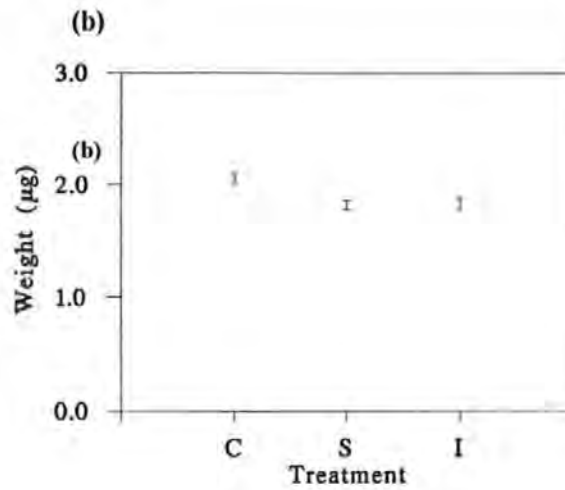
Figure 6.9: (a) Size and (b) weight of seeds from different "pollination" treatments (C = crossed, S = selfed, I = isolated). Bars show one standard error either side of the mean.
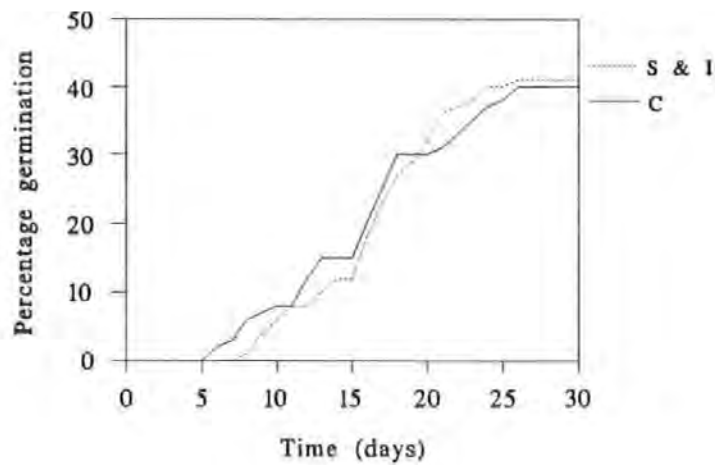
Figure 6.10: Germination rate of *L. urens* seed fertilized under three treatments (C = crossed, S = selfed, I = isolated) incubated at 29°C for thirty days.

6.3.3 Comparison of the plants performance in terms of vegetative and sexual reproduction

There was no variation in weighting between vegetative and reproductive structures of *L. urens* with grazing treatment in 1995, four years since the imposition of management. The ungrazed quadrats of compartment D had both the largest median rosette number and largest mean spike

height and Redlake followed second in both characteristics (Table 6.14).

	Median rosette number	Mean spike height
D(ug)	3	61
Redlake	2	53
D(g), C and A8	1	36 - 44

Table 6.14: Comparison of vegetative and sexual reproductive characters for plants at Redlake and within Andrew's Wood in compartments D (grazed (g) and ungrazed (ug)), C and A8.

6.3.4 *The effects of environmental variation on adult demography*

The effects of herbivores

There were no significant differences between defoliation treatment in terms of rosette number in July 1995 (Table 6.15 & Figure 6.11a). Defoliation exerted a significant effect on the leaf length and spike height of plants (Table 6.15). However, the difference was only manifested when the smallest plants (1 rosette) were clipped down to the 10 mm level (Figure 6.11b & c). Large plants (3-12 rosettes) and those clipped to the 20 mm level showed little variation in leaf length and spike height from controls (Figure 6.11b & c).

	d.f.	MS	F
Rosette number	2	7.91	0.90
Leaf length	5	1190.74	12.31***
Spike height	5	675.03	5.03***

Table 6.15: Results of three one-way ANOVAs on the effects of experimentally controlled spring defoliation on summer rosette number, leaf length and spike height. Degrees of freedom (d.f), mean squares (MS) and F-ratios are indicated.
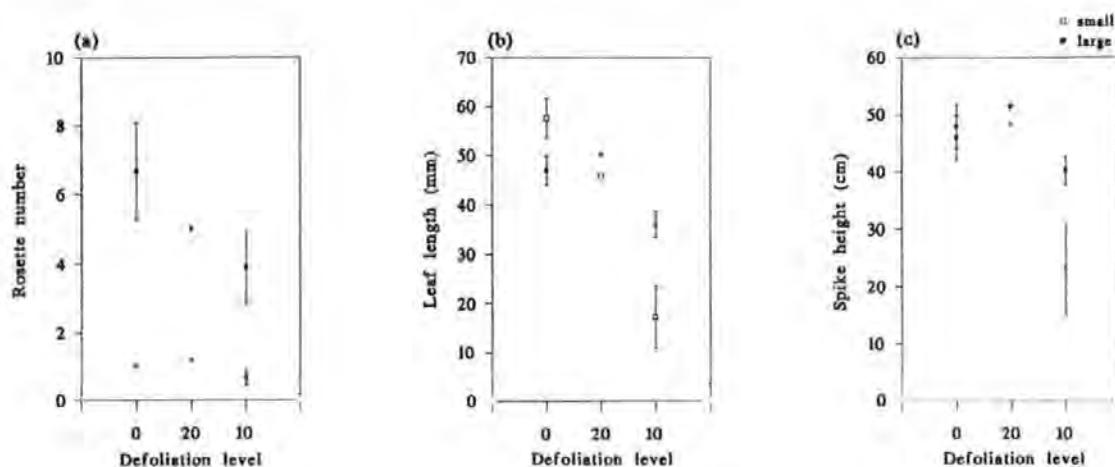
Figure 6.11: Effect of two levels of spring defoliation on plants of two size categories (small and large) (a) rosette number, (b) leaf length and (c) spike height in following summer. Bars show one standard error either side of the mean.

The effects of the light environment

The photosynthetic rate (mg CO_2 cm^{-2} h^{-1}) was ascertained using IRGA data in the following equation:

$$\frac{[\text{deflection (ppm)}][\text{flow rate}(mm^{-1})](44)(60\ 000)}{(1\ 000\ 000)(22.4)[\text{leaf area(cm)}]}$$

A monomolecular curve was found to give best fit to data (Causton & Dale, 1990). The light compensation point (irradiance at which photosynthesis just balances respiration) occurred at a low photon flux density and there was little variation in the photosynthetic rate between the first three light levels (1-20 μm photons m^{-2} s^{-1}) (Causton, personal communication)(Figure 6.12).

There was a difference in light quality between Redlake, Andrew's Wood and the compartments within Andrew's Wood (Figure 6.13). In the grazed areas of compartments C and D, Andrew's Wood, the mean red to far red ratio was always above 0.70 in both summer and winter, 1993 and 1994. There was more seasonal variation in the ungrazed areas, although light quality was similar in the winter. In summer, quality in ungrazed areas of compartments C and D and that of A8 and Redlake fell from unshaded (> 1.00) to around 0.50-0.60 (Figure 6.13). The quality of the light environment was significantly correlated with the height of the surrounding sward

(Table 6.16).
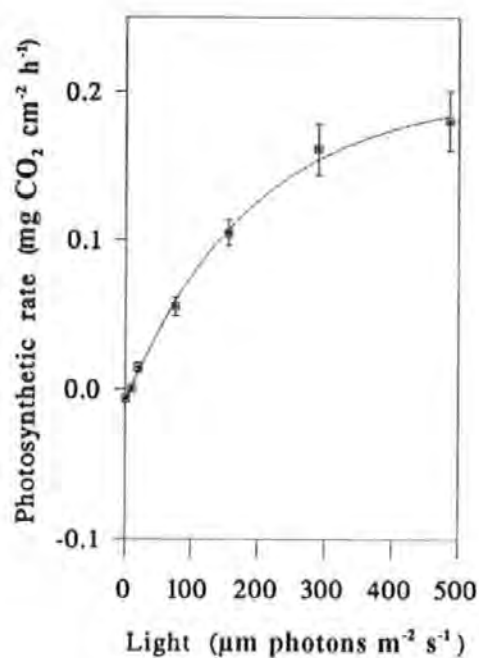
Figure 6.12: Variation in the photosynthetic rate of *L. urens* plants under six light intensities. Bars show one standard error either side of the mean.

Year	compartment	correlation coefficient
1993	C(g)	-0.14
	C(ug)	-0.72***
	D(g)	-0.48***
	D(ug)	-0.70***
	A8	-0.56***
1994	Redlake	-0.70***
	C(g)	-0.40**
	C(ug)	-0.71***
	D(g)	-0.57***
	D(ug)	-0.52***
	A8	-0.48***

Table 6.16: Spearman rank correlation coefficients of r:fr light reading and sward height within Andrew's Wood in compartments C and D (grazed (g) and ungrazed (ug)), and A8, 1993 and 1994 and at Redlake, 1994.
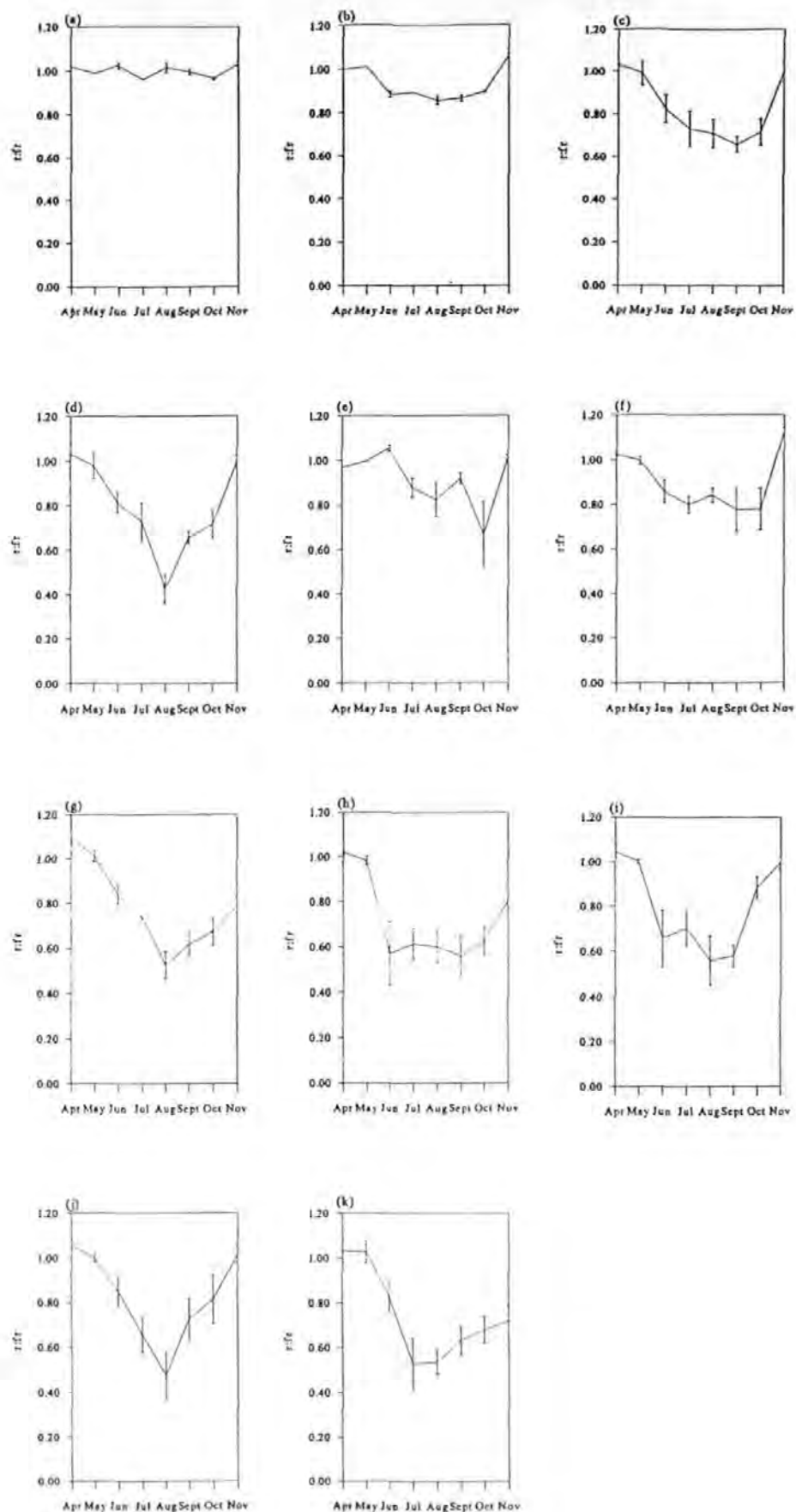
Figure 6.13: Variation in the quality of light reaching ground level from spring to autumn within (a) grazed compartment C 1993, (b) grazed compartment C 1994, (c) ungrazed compartment C 1993, (d) ungrazed compartment C 1994, (e) grazed compartment D 1993, (f) grazed compartment D 1994 (g) ungrazed compartment D 1993, (h) ungrazed compartment D 1994, (i) compartment A8 1993, (j) compartment A8 1994, (k) Redlake 1994. Bars show one standard error either side of the mean.

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6.4 Discussion

6.4.1 Growth and Longevity

The survival of *L. urens* after germination is very low in Britain. Thus, the flux of individual plants into and out of sub-populations is substantial in some sections of Andrew's Wood. Seedling survival is profoundly affected by season but the majority only survive for very short periods (section 5.3.1) and therefore they have little impact upon population processes. *L. urens* is a relatively long-lived perennial: of plants present at the end of the fourth annual census, 63% had been there initially, which was very similar to the retention of *Primula scotica* at 60% (Bullard *et al.*, 1987). Demographic studies have shown the populations of other rare perennial herbs to be even more static: 90% of *Peucedanum palustre* individuals remained over a period similar to this study (Meredith, 1978) and 75% of *Spiranthes spiralis* (Wells, 1981).

The counts of flowering spikes undertaken by the friends of Andrew's Wood and the Cornwall Wildlife Trust give a useful overview of the long-term trends in population size. The flux in spike counts closely matched the turnover of censused plants at Redlake 1992-1995. Both showed the population to be declining rapidly (Figures 6.1 and 6.3). The 40% increase in the number of spikes 1993-4 at Andrew's Wood (Figure 6.1) was, however, not a reflection of the change in the number of census individuals (Figure 6.3) and therefore must have been the result of an increase in the median number of spikes per plant at the reserve that year. Although it is necessary to be aware of the limitations of such data (section 3.3.1), the counts show the populations to be fluctuating widely, which is of interest for two reasons. First, such stochasticity increases the vulnerability of a population to extinction (Shaffer, 1981). Second, four years is a very short period on the time scale of these fluctuations and thus the demographic behaviour observed over the four-year census was likely to be specific to the populations during a particular part of their cycle, for example, recovery, decline or plateau (Law, 1981).

The lack of synchrony between population size at Redlake and Andrew's Wood and even

between the constituent parts of the Andrew's Wood population, despite similar habitats and associated communities (section 2.5.1) suggests that the fluctuations may be a result of major management events. This hypothesis is supported by the implementation of recent management that has been well recorded. The population in compartment C exhibited a pronounced response to scalloping from the first year it began in 1992. A lack of such favourable intrusion at Redlake has seen numbers fall dramatically since 1986, when a large scale scrub clearance was last undertaken.

Within compartment D of Andrew's Wood, the ungrazed quadrats supported more plants per m^2 than the grazed areas. There was, however, greater variation between compartments than between grazing treatments. Compartments D and A8 had much larger numbers of plants than C. There were so few plants in the quadrats of compartment C, that they were of little use in the grazing comparisons. All plants within the ungrazed quadrats of compartment C died during the census and very few remained in the grazed areas. Plants at Redlake (86%) and in the ungrazed quadrats of Andrew's Wood (65%) showed better chances of survival than the grazed quadrats of Andrew's Wood (29%). These lower death rates meant that initially the ungrazed areas had a higher density of plants but this density would not have been maintained. The proportion of emergence in the quadrats was falling and had reached zero after four years as a result of the very low germination and establishment success of *L. urens* in a closed sward (section 4.4 & 5.4).

At Redlake, the increase in median rosette number between 1993 and 1994 was due to the loss of a large number of plants with 1-2 rosettes when the ponies were grazing that year, rather than the result of individual growth. In contrast, plants in the ungrazed quadrats of D grew larger, both in terms of vegetative structures and inflorescence. Large plants are usually better equipped to survive and are more fecund (Clauss & Aarssen, 1994). The median rosette number was kept low in A8 by high emergence but there were many large plants. By comparison, the proportion of plants with four or five rosettes in the grazed area of compartment D was lower

than any of the other quadrats: plants in grazed quadrats did not reach such a large size as those in quadrats which were not grazed.

The growth of individuals in the ungrazed quadrats of Andrew's Wood indicated that *L. urens* must be tolerant of the crowded, ungrazed community. In particular, the red to far-red ratios reaching the basal rosette leaves of *L. urens* in these ungrazed quadrats during the summer months (June-September) were often as low as 0.50 or 0.60. Further support was offered from the IRGA results with the low light compensation point, little variation in photosynthetic rate between 1 and 20 μm photons $m^{-2}s^{-1}$ and low photosynthetic rate even under bright light, which together indicated *L. urens* to be a shade tolerance species (Salisbury & Ross, 1985). The results were more similar to the woodland *Veronica* species, *V. chamaedrys* and *V. montana* than *V. officinalis*, that is restricted to grassland habitat (Causton & Dale, 1990).

In ungrazed quadrats of Andrew's Wood, increasing rosette number meant improved survival chances. This relationship between size and survival was not as strong in the grazed quadrats, which suggested the input of an indiscriminate force. Defoliation only affected the very smallest plants when clipped to the 10 mm level. This defoliation was more extreme than grazing as tissue was only removed from *L. urens* and not from its neighbouring sward, which exaggerates the severity of the effects (Hendrix, 1988). Spring was also the most deleterious time for the defoliation, since *L. urens* depends on stored photosynthate for precocious early growth and in spring food reserves have been depleted (Wells, 1969; Staller & Serrao, 1983).

The major differences in adult demography seen between the grazed and ungrazed areas of compartment D must have been the result of physical damage, other than defoliation, which was incurred through the physical presence of the animal. Grazing animals frequently sit, lie, scratch and paw on the pasture in addition to walking, running and jumping on it (Spedding, 1971). These activities may damage the plants, usually in a patchy manner, but are not generally of major significance. Treading, however, can certainly influence both growth and

botanical composition of grassland through disturbance (Edmond, 1966, cited in Spedding, 1971). The degree of disturbance varies with the structure of the sward, the nature of the soil, and some plant species are more susceptible to the direct physical effect of poaching than others (Crawford & Liddle, 1977). Hooves not only possess sharp cutting edges but they carry the weight of the animal on a very small surface area. This results in surprisingly high downwards pressures when ungulates walk e.g. Jersey cattle 1280-1460 g cm^{-3}, South Devon cattle 1430-1600 cm g^{-3} (Kubo & Isobes, 1975). *L. urens* appeared to be a sensitive species and further support for this was offered from incidental observations at Redlake. Many established plants were lost during the winter graze of 1993-4, but very few plants were seen to have been defoliated. This avoidance was more likely to be due to the small vegetative size of over-wintering plants rather than active preferential grazing. Cattle have little fine-scale control in plant selection from an intimately mixed sward (Harper, 1977)

Studies of rhizome development have shown that the dimensions of the rhizome cannot be predicted from the plants age or vegetative size in *L. urens*. The dimensions of individual rhizomes are continually changing as the plants may divide beneath ground into a number of physiologically independent modules. This splitting protects against disease, but prevents resource sharing (Harper, 1978). There was no correlation between the number of rosettes and the number of divisions in the rhizome of *L. urens*. Hence, in the field, there was a problem with using rosette number as a measure of plant size, since the meaning of rosette number was not fully understood. It was not possible to predict the number of individuals that made up the local clusters of rosettes and it was necessary to treat them as one plant. The number of divisions in the rhizome may increase with age: there was an increase in the number of divisions between plants in their first and second year. However, the experiment was not continued and results were inconclusive.

6.4.2 *Reproduction*

L. urens produces a large amount of minute seed. The development of most angiosperm seeds can be divided into two stages: enlargement and filling (Bewley & Black, 1994). Enlargement is the result of cell division, followed by an influx of water which drives cell extension. Filling occurs as the reserves are deposited within the endosperm. The seeds of *L. urens* are very small and therefore contain few reserves (Bryant, 1985). Length and depth were fixed at an early stage of development (personal observation) and seeds formed flat discs. Presumably this form coincided with embryonic development, as later seeds swelled to their final weight and width. Seed weight was the most constant of all the reproductive measures taken of *L. urens*. Instead, variation in maternal resource status was reflected in seed number which was consistent with findings for *Lobelia cardinalis* (Devlin, 1988) and a large number of weedy species (Harper & Gajic, 1961; Palmblad, 1968; but see Harper *et al.*, 1970 for a review). Seed size, within a species, is genetically controlled to a very narrow optimum (Harper *et al.*, 1970). Seed weight is often correlated with seedling weight (Gross, 1984; Zhang & Maun, 1993; Gonzalez, 1993) and establishment success (Cideciyan & Malloch, 1982; Morse & Schmitt, 1985; Houssard & Escarre, 1991). Therefore, fewer normal sized offspring have a better chance of survival than the combined prospects of a large number of 'runts' (Lack, 1954; Cody, 1966). These advantages are offset by the fact that larger seeds do not disperse as far (Morse & Schmitt, 1985; Willson, 1992; Thompson, 1993b) and may be more apparent and valuable to herbivores (Janzen, 1969; Silvertown, 1982; Crawley, 1983; Fenner, 1985; Louda, 1989) than small seeds.

Variation in seed number was accommodated through change in number of seeds per capsule rather than through number of capsules per plant. In some species, the number of seeds in a capsule is controlled through nectar production (Pleasants, 1983; Devlin *et al.*, 1987), whereas in others, seed abortion plays a major role (Bawa & Webb, 1984; Marshall & Ellstrand, 1985). The similar fecundity of plants at Redlake and Andrew's Wood over two years is of interest. Redlake and Andrew's Wood were grazed at very different intensities over the study period and the relative importance of fecundity over vegetative growth has been seen to increase with

grazing intensity (Murphy, 1968; Schaffer, 1974). However, this study predicts little difference in the fecundity of *L. urens* with grazing treatment.

L. urens shows indeterminate reproductive development and in both 1993 and 1994 at Andrew's Wood, the lower section of the inflorescence, which was flowering in July, was of primary importance in terms of seed production. Capsules produced later in the year contained fewer, smaller seeds. These later seeds may not have had sufficient time to reach maturity or their flowers may have functioned primarily as pollen donors (Ehrén, 1991). At Redlake, however, although the terminal capsules contained fewer seeds, these were larger than those produced earlier in the year. Variation in seed size and morphology with position on mother plant, and even with position in fruit has been seen in a great number of species including *Lobelia cardinalis* (Devlin, 1989) (see Gutterman, 1992 for a review) and is of interest, although in this study it was not important to the overall fecundity of the two populations. The timing of flowering at Redlake and Andrew's Wood was synchronous (personal observation), and it was unlikely, therefore, that the difference was a result of climatic variation. Fertilization may have provided the variation, as cross-pollinated seed was longer than selfed seed. The vegetation at Redlake, being denser than Andrew's Wood, could have restricted pollinators and thus the lower seed would be predominantly self-fertilized. However, were this the case, more empty capsules would have been expected, as seen with isolated plants in pollination experiment. Work on *Eichhornia paniculata*, which, like *L. urens*, is a self-compatible entomophilious species with a vertical inflorescence, has shown that the behaviour of the pollen vector affects the distribution of crossed and selfed seed on the inflorescence. *E. paniculata* is bee-pollinated and the bees foraged upwards on inflorescence which increased in the fraction of self-fertilized seed from bottom to top flowers within an inflorescence (Barrett *et al.*, 1994). The major pollinating species may have varied between Andrew's Wood and Redlake and thus have produced the variation in seed size with floral position. Little is known about the pollinating species, but if *L. urens* was visited by a positively geotactic pollinator at Redlake and by a negatively geotactic species at Andrew's Wood, then this would have produced a similar pattern. Flowers at Redlake

would have increased chance of cross-fertilization higher on inflorescence and flowers at Andrew's Wood, lower on inflorescence. *L. urens* is not a mass bloomer, only a few flowers open on a spike at any one time, but the general distribution of crossed and selfed seeds is feasible (Plate 6.3). Alternative hypotheses for this variation in seed size with position on inflorescence are possible. First, that the denser vegetation of Redlake reduced heat and light which limited seed ripening. Shaded branches of *Lindera benzoin*, an understory shrub, produced lighter seeds than those exposed to full sun (Niesenbaum, 1993) and a reduction in yield accompanied the shading of *Zea mays* L. (Earley *et al.*, 1967). Variation in the environment with depth in sward might be a possible explanation for difference in seed weight but not length. Second, seasonal environmental stress during the development of these early seeds could have temporally restricted resources available for seed investment. Interpretation must be carried out with caution, as Redlake data are from one year's seed production.

The analyses of the variation and correlations of fecundity with plant morphology revealed a number of relationships, many of which were not consistent between Andrew's Wood and Redlake, or between data collected in 1993 and 1994. The fecundity characters that were most plastic in response to resource status, as opposed to those that were invariably constant, were not pre-established and, therefore, a large number of correlations were undertaken. The derivation of a definative result was difficult using correlation techniques as, firstly, correlation does not imply causation and, secondly, a large number of data sets were analysed for associations, hence the chance of spurious correlation was high.

At Andrew's Wood, inflorescence size was strongly correlated with capsule number and seed number. Larger inflorescence would be expected to yield more capsules and daily inflorescence size, the number of flowers open on a particular day, has been seen to increase seed number through pollinator attraction in many species of various life-forms from the herbaceous shrubs *Hybanthus prifolius* (Augspurger, 1980) and *Aralia hispida* (Thompson, 1988) to the evergreen *Metrosideros collina* (Carpenter, 1976) and the perennial herbs *Ipomopsis aggregata* (De Jong *et*

al., 1992) and *Eichhornia paniculata* (Barrett *et al.*, 1994).

Vegetative size in plants reflects maternal resource status and hence is often correlated with reproductive output (Aarssen & Clauss, 1992). Therefore, it was surprising that there were no correlations between vegetative size and fecundity at Andrew's Wood in either 1993 or 1994. This could result from the dividing of the rhizomes, with rosette number representing a measure of parental resource status but not a measure of the resource status of individual clones which may have split from the parent plant. At Redlake, all of the vegetative morphological characters investigated were strongly correlated with seed length and there were no other correlations with measures of fecundity. There may be a connection between the proportionately longer seeds of the terminal capsules and the correlation between large plants and long seeds at Redlake, but verification would require a specifically designed study.

The complex variation and correlations of the seed yield of *L. urens* at Andrew's Wood over the two years show that the reproductive allocation of plant populations can vary over a very small spatial and temporal scale. Many studies have shown substantial variation in demographic parameters induced by small-scale variation in the environment or merely from one year to the next. The reproductive allocation of *Plantago coronopus* varied with plant density within populations (Waite & Hutchings, 1982) and in a 10-year study the rates of clonal growth and seed production of the wild daffodil (*Narcissus pseudonarcissus*), within an ancient woodland in Cumbria varied with woodland management (Barkham, 1980a; b). Mack & Pyke (1983) saw little inter-population variation for *Bromus tectorum*. The major flux in the reproductive parameters of all three study populations resulted from annual environmental variation in climate, and predator density and variation in reproductive parameters of *Arisaema triphyllum*, a forest perennial, were also seen to vary as a result of year to year environmental variability (Bierzychudek, 1982). Unfortunately, an underlying assumption of many demographic analyses is that parameters do not vary with time and space and this can lead to mistaken conclusions about the demographic status of a species (Moloney, 1988).

L. urens is entomophilous (Brightmore, 1968). A loose raceme, small flowers and purple petals together suggest that Diptera may be common visitors (Proctor & Yeo, 1973). This was confirmed by Brightmore (1968), who found that Syrphidae were particularly common pollinators. Microlepidoptera (Swanson, 1991), large (*Ochlodes verata*) and small (*Thymelicus sylvestris*) skippers (Spalding, personal communication) (Plate 6.3) and *Plusia gamma* (Brightmore, 1968) have also been seen nectaring on *L. urens*.

(a)   (b)

Plate 6.3: (a) *Ochlodes verata* and (b) *Thymelicus sylvestris* nectaring on *L. urens* at Redlake (Photographs taken on 10.7.92 by A. Spalding).

Although the frequency of pollinator visits in unknown, hand pollinated plants produced similar numbers of seeds to plants in the field in 1994, which indicated that seed production was not pollen limited. Isolated plants produced few seeds as *L. urens* partially guards against autogamy by the temporal separation of pollen and stigma maturity (Brightmore, 1968). There are very

few species with hermaphrodite flowers, where it is completely impossible for pollen to reach the stigma of the same flower and if insect visits fail, it is usual for at least some self-pollination to take place (Proctor and Yeo, 1973). Furthermore, structural features do not decrease the probability of a flower receiving pollen from another on the same plant. Rather, protandry increases the chance of geitonogamy, since it allows fresh pollen to fall from younger flowers directly onto those older ones with receptive stigmas below, and this geitonogamy is genetically no different from autogamy (Proctor & Yeo, 1973).

L. urens displayed a high level of self-compatibility. Fewer seeds were produced by isolated plants, since less pollen was introduced to the stigma but manual self-pollination did not reduce seed yield or decrease germination. However, seed was lighter than cross-pollinations. Classic studies of pollination presumed that self-compatibility was controlled by a single allele and that plants were either capable of self-fertilization or completely resisted it, in other words, seed set following self-pollination and fertilization was generally considered to be a demonstration of self-compatibility (Weller, 1994). As more studies have been undertaken, it has become increasingly clear that there are many degrees of self-compatibility (Crowe, 1971; Galen & Kevan, 1980). Even if, as seen here, full seed set is achieved upon exclusive self-fertilzation, weak self-incompatibility reactions may be present that are only detectable when foreign pollen competes with self pollen of its own stigma, a condition defined as cryptic self-incompatibility (Bateman, 1956; Seavy & Bawa, 1986; Bertin & Sullivan, 1988). Besides such incompatibility phenomena, there are also post-zygotic inbreeding effects of partially self-fertilizing species (Charlesworth & Charlesworth, 1987; Barrett, 1988). A much more useful insight into the self-compatibility of *L. urens* may have been gained had self-fertilized seedlings been grown on to observe for depression of establishment and growth. If self-fertilization occurs over several generations, the individuals arising are homozygous and natural selection is not effective (Lewis, 1979) and, in theory, less critical levels of self-fertilization can lead to inbreeding depression (Charlesworth & Charlesworth, 1987). Self-fertilization could explain the poor establishment success of *L. urens* seedlings at Redlake and Andrew's Wood.

Herbivore exclusion at Andrew's Wood provided a very shady habitat and limited the recruitment of *L. urens* from seed (sections 4.4 & 5.4) but it afforded the best environment for large, robust and fecund adult plants. Over the four years of census, the ungrazed constituents of the population at Andrew's Wood showed a regressive structure with little emergence and a high proportion of large plants. Although grazing through until spring at Redlake created large gaps in the vegetation (section 4.3.2 & Figure 4.10) that facilitated emergence (section 4.3.2 & Figure 4.8), none of the seedlings survived more than two months (section 5.3.1). This was partly a result of the timing of their emergence, but the short growing season was accentuated by the low summer light quality. The light quality at Redlake following the graze was still as low as the ungrazed areas of Andrew's Wood (Figure 6.13), probably because the removal of the *Betula* scrub was ineffective (personal observation). The establishment of seedlings was most successful in the winter grazed areas of Andrew's Wood. The presence of herbivores feet are essential for the recruitment of *L. urens* but the same presence limits the growth and survival of the adult plants. Irrespective of grazing treatment, at both Andrew's Wood and Redlake, *L. urens* was very fecund.

SEVEN

Seed ecology

7.1 Introduction

The potential for recruitment from seed depends upon the efficiency of dispersal and the ensuing fate of the seeds. Poor dispersal, excessive losses to predators or pathogens and the paucity of successful emergence from the seed bank may all limit the population density of *L. urens*.

The dispersal of seed may serve several functions. Efficient local dispersal to "safe-sites" avoids competition between seed and parent (Harper, 1977) or inbreeding (MacDonald & Smith, 1990) and provides an escape from density or distance-responsive seed predators (Janzen, 1969), pathogens (Augsperger & Killey, 1984) and parasites (Willson, 1992). Failure to reach such 'safe-sites' may restrict the germination and establishment of seedlings (Grubb, 1977; Harper, 1977). Long-range dispersal is required for the colonisation of new areas and thus is becoming increasingly important in the face of severe habitat fragmentation. The dispersal characteristics of a species give an indication of the degree of habitat permanence and disturbance to which it is most suited (Hodgson & Grime, 1990). Long-range dispersal is of particular importance to early successional species for reaching the sporadically opening patches or disturbed habitats they require, whereas dispersal efficiency is less critical in more stable communities (Ridley, 1930; Howe & Smallwood, 1982; Sacchi, 1987). Clearly, seed dispersal is a critical stage in the life-history of plants and the study of plant population dynamics (Harper, 1977; Sacchi, 1987; Thompson, 1993b).

The fates which may befall seed, once it lands on the soil, can be categorized broadly as: to germinate, be dormant, form a seed bank, or die (following Harper, 1977). The phenology of

dispersal has a profound effect on its efficiency and the ensuing fate of the seeds. Ideally, seed maturation and dispersal would be timed to match availability of dispersal agents and good germination conditions, but these ideals are constrained by selection for flowering time as well as period required for fruit maturation (Willson, 1992).

Most plants produce an enormous amount of seed but exhibit a paucity of emergent seedlings (Sarukhán, 1974; Sagar & Mortimer, 1976; Watkinson, 1978; Crawley, 1992). This leaves the fate of the majority of seeds undetermined. Cavers (1983) suggests that the highest rates of mortality for many species occur at the seed stage. The factors responsible for the depletion of seed from the soil are not well understood (Warr et al., 1992). In the absence of other evidence, the fate of most seed in the soil is assumed to involve degradation by microbial decomposers or by seed-ingesting soil fauna, although viability may have been lost earlier through molecular oxidative processes (Hutchings, 1986; Hendry, 1993a). The chemistry of seeds plays an important role in their differential fate (Baker, 1989). Research carried out on the chemical defences of seed against herbivores and soil micro-organisms has shown that many seeds contain protective chemicals in their coats (Forrest & Bendall, 1969; Warr et al., 1992; Hendry, 1993b; Hendry et al., 1994).

A seed bank is the reservoir of buried seeds in the soil (Harper & White, 1971). Viable seeds falling from the parent plant will enter the seed bank if they do not either germinate on the surface or succumb to the attack of predators or pathogens (Harper, 1977). Incorporation into the soil occurs slowly by burial beneath litter (Oosting & Humphreys, 1940) and by integration during natural soil movement aided by water percolation (Hutchings, 1986), or more rapidly because of the activities of soil animals (McRill & Sagar, 1973; McRill, 1974; Harper, 1977). Once in the soil, seed varies in its persistence (Thompson & Grime, 1979; Thompson, 1993a). The seed of some species is transient, lasting only a year or so, whereas other very persistent seed is able to remain in the soil for an almost infinite number of years, awaiting suitable environmental conditions (Thompson & Grime, 1979).

Seed banks have been the object of much research which has been extensively reviewed (e.g. Kropáč, 1966; Harper, 1977; Grime, 1979; Cook, 1980; Roberts, 1981; Vyvey, 1988; 1989; Leck *et al.*, 1989; Warr *et al.*, 1993). Any attempt to discuss the population dynamics of an individual species in the context of its conservation must include quantified studies of the seed bank (Parone & Reader, 1982), since the bank represents a demographic reserve of propagules which dampens between year fluctuation in population size, thereby reducing the risk of stochastic extinction (Sarukhán, 1974; Baskin & Baskin, 1978; Brown & Oosterhuis, 1981; Harper, 1981; MacDonald & Watkinson, 1981; Leck *et al.*, 1989; Levin, 1990; Baskin & Baskin, 1991; Given, 1994). A long-lived soil seed bank also embodies a reserve of genetic variability for a population and hence increases the range of genotypes on which natural selection can act (Gottlieb, 1974; Harper, 1977; Baskin & Baskin, 1978; Lande & Barrowclough, 1987; Baker, 1989; McGraw, 1993). Such diversity could have important evolutionary consequences (Levin & Wilson, 1978; Leck *et al.*, 1989), particularly if the adult population is severely depleted, when diversity may provide a buffer against genetic drift and bottle-necking (Levin & Wilson, 1978; Levin, 1990). In larger populations, however, this genetic memory may be detrimental to population growth dynamics by adding material maladapted to the present environment (Levin & Wilson, 1978; Bennington *et al.*, 1991). A seed bank also offers a second chance, when the above ground population goes extinct (Moore, 1983): populations which have been considered extinct can still be recovered from seed which has remained dormant (e.g. Walters, 1974; Rowell *et al.*, 1982; Rowell, 1984).

Seed from *L. urens* is very small and does not possess any specialised morphological attributes for wind or animal dispersal (Plate 1.1a). The character which has been used most frequently to quantify the dispersability of such seed is their terminal velocity. Slow-falling seed shows improved dispersal through a longer exposure to the wind (Sheldon & Burrows, 1973; Sheldon & Lawerence, 1973; Augsperger, 1986; Green & Johnson, 1990; Schulz *et al.*, 1990; Andersen, 1991; Thompson, 1993b). Terminal velocity, chosen for its ease of determination in the laboratory, is simply the rate of fall of seed under negligible air currents. The method allows

the height seed is released to be altered and a greater height is known to improve dispersability (Sheldon & Burrows, 1973; Burrows, 1975). Results obtained using this method must be treated with caution. Seed will rarely be dispersed in still air conditions (Hutchings, 1986) and may demand a specific minimum wind speed for release (e.g. Meredith, 1978). Indeed, given variable wind speed, the terminal velocity of seed is not correlated with the final distance the seed attains (Morse & Schmitt, 1985). Moreover, the wind dispersal distances achieved by seeds are also influenced by vegetation obstruction and topography. Secondary transport of seeds along the soil surface must also be taken into account (Matlack, 1989). Seeds can be moved across the soil by both wind and water but the most efficient vectors are animals. For example, ants can move individual seeds up to 37 cm per day (Mortimer, 1974).

Previous workers have employed two field methods which provide a fuller, more accurate picture of seed dispersal than purely a measure of terminal velocity. The first, entrapment of seed as it reaches the soil (e.g. Levin & Kerster, 1969; Werner, 1975; Meredith, 1978; Marlette & Andersen, 1986), includes the obstruction by vegetation as a factor influencing dispersal distance, but gives a misleading picture since the secondary dispersal is restricted. The second method follows individual seeds from source to landing (e.g. Watt, 1919; Yocom, 1968; Levin & Kerster, 1969; Platt, 1975; Morse and Schmitt, 1985) and this tracking can be assisted with the use of dyes or radioactive traces (e.g. Werner, 1975; Watkinson, 1978). This provides the most complete picture of dispersal efficiency but such studies only have a reasonable recovery level if the majority of the dispersal distances are short and the technique is not, therefore, suitable for studies of long-range dispersal. A combination of seed tracking in the field and a laboratory-based dispersability study provides the fullest results of short-range dispersal ability (e.g. Morse and Schmitt, 1985). With regards to local dispersal, however, it is generally felt that most seeds fall in leptokurtic distributions in relation to the parent (Sheldon & Burrows, 1973; Levin and Kerster, 1974; Werner, 1975; Marchand & Roach, 1980; Hutchings, 1986; Suzuki & Kohyama, 1991; Willson, 1992) with the majority moving only short distances, within 1 m^2, from the mother plant (Sheldon and Burrows, 1973; Silvertown, 1982; Fischer, 1987). In

contrast to the majority of contemporary studies, classic surveys of seed dispersal (Ridley, 1930; van der Pijl, 1969) were far more concerned with the rare events of long-distance colonisation than quantifying the day-to-day happenings in more normal ecological situations. The role of animals, particularly birds, in transporting occasional founders to new sites is probably very significant (Silvertown, 1982; Schemske et al., 1994). These incidents are very important to colonisation but are extremely difficult to quantify.

The seed of L. urens can be hypothesized as being long-lived and forming a large bank below extant populations. Its small and compact shape is associated with reduced rates of decay (Toole & Brown, 1946; Harper et al., 1970; Fenner, 1985; Thompson, 1987; Thompson et al., 1993). Furthermore, the acidic, waterlogged habitat characteristic of L. urens is known to be conducive to long seed life (Champness & Morris, 1948; Lewis, 1961; Schafer & Chilcote, 1970; Hodgson & Grime, 1990). Additional support is provided by historical records: L. urens reappeared at Yarner Wood NNR, Devon in 1958 after thirty years of absence (section 2.2.1); Archibald (1971) reported the possibility that any soil disturbance will lead to resurgence of L. urens for at least thirty years after the last plant has died; Brightmore (1968) stated that seed stored at room temperature remained viable for eight years and viability in the soil would certainly be much longer.

This study of the seed ecology of L. urens concentrated upon two factors which are of interest; the density of germinable seeds below an extant population and the persistence of seeds in the soil.

7.2 Methods

7.2.1 The bank of L. urens seed below an extant site

Seeds are irregularly clustered within the soil, both in the horizontal and the vertical plane (Thompson, 1986; Bigwood & Inouye, 1988; Dessaint et al., 1991; Lavorel et al., 1991).

Workers agree that a large number of soil samples must be collected in order to overcome the variation in seed content and to obtain a stable estimate of density (Champness, 1949; Rabotnov, 1958; Kropáč, 1966; Roberts, 1981; Thompson, 1986; Benoit *et al.*, 1989; Gross, 1990). Exactly how many samples are required is under debate and ranges from 200 (Champness, 1949) to 15 (Gross, 1990). In this study, only 15 samples were taken since enumerating the seed from such a large number of samples is labour, time- and space-intensive (Thompson, 1993a). Although more samples would be needed to ensure precise estimates of seed density, sufficient were taken to test the hypothesis that *L. urens* forms a large seed bank.

The time of year at which samples are taken can have a marked effect on results. In this survey samples were collected on March 8 1993, since spring sampling allows seeds to be naturally chilled overwinter, thus reducing error through dormancy (Raynal & Bazzaz, 1973; Leck & Graveline, 1979) and also catching seed before the germination peak in May-July (Warr *et al.*, 1993).

Sample points were located at random with the southwest corner of compartment D of Andrew's Wood, an area densely occupied by adults. A bulb planter (see Warr, 1991) was used to remove soil cores of 6 cm diameter and 10 cm depth. Soil was washed from the tool between taking each sample to minimise transferal of *L. urens* seeds. Each core was subsequently divided into two sections, representing depths of 0-5 cm and 5-10 cm, giving a total of 30 samples representing an area of 424 cm^2.

There are two widely adopted techniques for estimating the composition of seed banks. The most suitable to study the bank of *L. urens* seed involved glasshouse incubation of the soil followed by identification and enumeration of emergent seedlings to determine the density of germinable seeds in that sample (Brenchley & Warington, 1930; Champness, 1949; Major & Pyott, 1966). The alterative technique requires seeds to be isolated from the other material by floatation and subsequently, their viability to be tested by staining with tetrazolium salts (e.g.

Malone, 1967; Moore, 1972). This method is not suitable for small seed (Roberts, 1981; Moore, 1972; Hutchings, 1986). Perhaps the greatest defect of the method chosen results from the selective germination imposed upon seeds in the glasshouse (Major & Pyott, 1966; Malone, 1967; McGraw *et al.*, 1991; Brown, 1992; De Villiers *et al.*, 1994). The density estimate may be less than the actual density and it is generally accepted that an unknown number of viable seeds do not germinate (Thompson & Grime, 1979; Thompson, 1986).

The soil was broken up and the stones and roots removed with the use of a coarse (1 cm) sieve. No chilling treatment was applied. The samples were spread out on the seed trays over a layer of sand and placed in a glasshouse. The glasshouse provided thermostatically controlled minimum heating as a precaution against late frosts and continual watering from below by capillary matting linked to a automatic reservoir. A further seed tray containing sterilized potting compost was provided as a control to detect any wind dispersed seed, although, in the event, none were found. Once germination began, seedlings were identified and removed at intervals over a 49 day period (following Thompson & Grime, 1979). With practice and the aid of Chancellor (1966), Hanf (1974), and Muller (1978), it became possible to identify virtually all seeds at an early stage of development. Unidentified seedlings were transferred into pots and grown, where necessary, until flowering. The samples were stirred on April 5, 28 days after commencement, to increase germination (Hill & Stevens, 1981; Forcella, 1984). A germination pulse occurred after 14 days, few germinated between 28 and 41 days and germination was negligible after 41 days. It is possible that more seeds may have been discovered if the soil had been kept longer (Roberts, 1981; Brown, 1992). The decision to terminate was made, since the detection of *L. urens* was the main focus of this trial and emergence of this species had occurred solely within the first two weeks of the experiment.

	Seed density (m^{-2})	
Species	0-5cm	5-10cm
Cardamine pratense	71	-
Circium arvensis	142	142
Circium palustre	213	-
Lobelia urens	**12425**	**5112**
Lotus uliginosus	-	71
Lysomachia nemorum	2983	1491
Plantago lancolata	3555	213
Prunella vulgaris	639	42
Pulicaria dysentrica	1633	71
Ranuculus flamula	284	994
Ranunculus repens	71	-
Veronica montana	994	355
Veronica persica	1349	127

Table 7.1: The number of germinable seeds (per m^2 of surface area) at Andrew's Wood, 0-5cm and 5-10 cm soil depths.

7.2.2 The persistence of L. urens seed in the soil

To date, a method for estimating the longevity of buried seeds by censusing individuals has not been devised (Hutchings, 1991). It is possible to monitor the emergence of seedlings in an area into which the immigration of fresh seed is prevented (e.g. Roberts, 1962; Sarukhán, 1974) but such work must, by its nature, be long-term (Moore, 1983). The rate of loss of seeds from samples sown into sites, or cohorts of seeds have been calculated by spraying the seeds with paint or dye, or radioactive labelling (e.g. Watkinson, 1978) but this is not suitable for small seed in dense vegetation. A more frequently used technique entails burying fresh seed and retrieving samples at intervals e.g. Dr. Beal's experiment (Kivillan & Bandurski, 1981). This can also be a lengthy process but it does lend itself to adaption. Conn (1990) monitored the annual losses in viability incurred in seeds buried over five years and used this to estimate longevity.

A definitive way to test the hypothesis that *L. urens* has a long-lived bank is to sample below an extinct population. A suitable site must have held a self-sustaining population for a number of years to ensure a bank of seed had accumulated and have been isolated from any fresh seed source since the extinction of that population. Yarner Wood NNR, Devon provided the most promising option for fulfilling these criteria (section 2.2.1 contains a site history). The site is owned and managed by English Nature. *L. urens* reappeared in 1958-1968 in four locations all within a 15 m radius, covering a total area of 100 m². These locations were accurately mapped at the time and are identifiable by means of compass bearings from a fixed point post. One hundred samples were collected on June 8 1993, 25 from each of the former locations. The samples were randomly located and removed using the same method employed previously at the extant site. Due to the poor structure of the soil, lack of moisture and the large amounts of stone and roots present, it was not possible to separate the core into two depths.. Samples were bulked together distinguishing between the litter and soil and the four quadrats to give twenty aggregate soil samples and eight aggregate litter samples representing a total area of 2827.4 m². The methods of soil preparation follow that described earlier. The seed trays were placed in a polythene tunnel and watered from above at least twice a day, and more frequently when necessary. The trial ran for 12 months and was terminated on June 6 1994.

No germinable seed was detected in the soil, 25 years after extinction. This is an unexpected result, since historical evidence suggests that the seed of *L. urens* persists for longer than twenty-five years (Archibald, 1971). The seed bank may have been too small or too highly aggregate, as a result of poor dispersal, to be detectable by the sampling method employed.

7.3 Discussion

There has not been a formal study of the dispersal ability of *L. urens* but existing evidence strongly suggests that the seed is adequately dispersed locally to reach suitable safe sites. The height of the associated plant communities, averaging 40 cm (Table 2.3) combined with large

quantities of *Molinia caerulea* litter (Table 2.3) may obstruct seed from reaching the soil surface (Andersen, 1967; Fowler, 1988). However, the seeds of *L. urens* are very dispersable in wind, simply by virtue of their small size (see Willson, 1992; Thompson, 1993b) and are held at least as high as the surrounding sward thus further facilitating dispersal. Furthermore, lying dormant in the soil facilitates the seeds dispersal in time and is often a substitute for dispersal in space (Harper *et al.*, 1970).

Today, *L. urens* is restricted to six locations along the south coast of Britain (section 2.2), although there are many other very similar possible locations in the region (section 2.6). The lack of obvious structural modifications to aid dispersal may hinder colonisation of these disjunct but potentially suitable habitats. Indeed, the habitats of *L. urens* are bordered by woodland (section 2.5), which may interrupt any long-range dispersal. The rarity of such events deems their study impossible; Little Bradley was the only recorded successful colonisation of a new site in the last 50 years.

The dispersal of *L. urens* seed in Britain is ill-timed. The erect capsule dehisces by two apical pores throwing the seeds out a short distance (Brightmore, 1968). Often, however, this autochory is very inefficient, especially in the absence of dry weather, and a large number of seeds remain in the capsule for months until disintegration of the thin parts of the wall permits their dispersal (Brightmore, 1968). Alternatively, the whole flowering spike falls to the ground with many of its capsules still intact (personal observation). In Portugal, *L. urens* sets seed in early June (Daniels, personal communication) but in Britain, restricted by a shorter growing season, seeds are not ripe until early September. By this time, it is often too late for the fine weather necessary to promote dehiscence and also too late for those seeds which germinate immediately to establish (section 5.3.1). Poor dispersal is not a problem in itself as the enormous seed bank dispenses with the requirement for effective local dispersal.

Over the two-year detailed demographic study (section 3.3.2), although *L. urens* produced an

enormous amount of seed, few emerge as seedlings (section 4.3.2). A great many studies have documented the impact of predation on plant fecundity (see Silvertown, 1982; Louda, 1989 and Crawley, 1992 for a review). These show that the most vulnerable seeds are large, conspicuous, high energy packages (Louda, 1989) and that active predation of such small seed as that of *L. urens* is unlikely (Janzen, 1969; Silvertown, 1982; Crawley, 1983; Fenner, 1985). Furthermore, should accidental consumption by indiscriminate grazers occur, small seed can pass through the digestive system and still remain viable (Stainforth & Cavers, 1977). Seed which does enter the bank may succumb to pathogen attack. The chemistry of the seed coat of *L. urens* has not been investigated, but persistent seeds usually do not have chemical defences (Janzen, 1969). Many *L. urens* seeds that fall to the ground still encapsulated may have an increased incidence of fungal attack from the multitude of organisms already living on the capsule but the number of seeds which enter the bank indicates that this is not a significant fate.

The estimates of the size of the seed bank of *L. urens* are of a staggering magnitude (Table 7.1). It was four times greater than any other species in the samples and over 17 times greater than the most common species found by Thompson (1986) below his acidic grassland in Devon *(Danthonia decumbens* with 703 seeds m^{-2}). The quantity of *L. urens* is more comparable with Chippendale & Milton's (1934) estimate of *Calluna vulgaris* beneath a hill pasture dominated by *Nardus stricta* in Wales (ca. 12000 seeds m^{-2}) and other pasture species (3700-55000 seeds m^{-2}, Parone & Reader, 1982). Although the estimates of seed densities may be imprecise due to the small number of samples taken, *L. urens* obviously has a large buried seed population.

L. urens forms a persistent seed bank. The experiment at Yarner Wood did not confirm this but the observation of seeds in the lower strata (5-10cm depth) below the extant population at Andrew's Wood gives an indication of its persistence (Chippendale & Milton, 1934; Moore & Wein, 1977; Kellman, 1978; Hill & Stevens, 1981; McGraw, 1987; Thompson, 1993a). Short-lived seeds lose their viability before reaching the lower soil layers and tend to be present only near the surface whereas long-lived seeds occur in both the upper and lower layers (Warr *et al.*,

1993). Further support is provided by a predictive tool based on the aforementioned relationship between seed size and persistence in the soil using forty British species (Thompson, 1993a; Thompson *et al.*, 1993). When the weight of the seeds are plotted against the variance of their three linear dimensions, persistent seeds consistently appear in the lower left region of the figure (Figure 7.1). Using the size averages from over 1000 seeds from Andrew's Wood (section 6.3.2), this index places the light and compact *L. urens* seed, well within the domain of those which persist over five years (Figure 7.1).
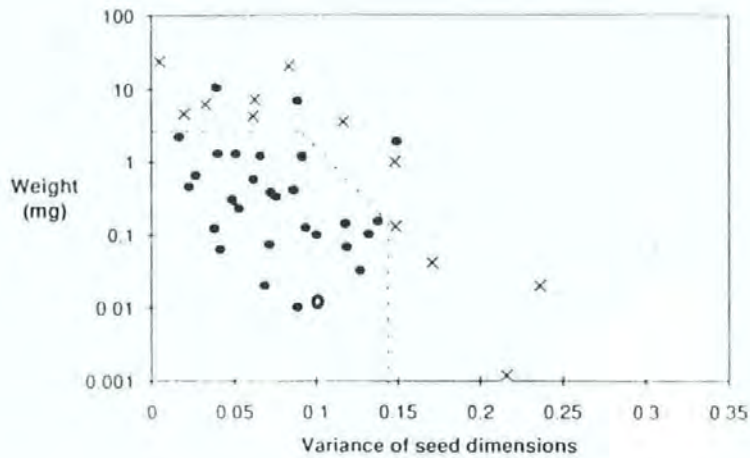
● species with persistent seed banks,   × species with transient seed banks,   o *L. urens.*

Figure 7.1: Weight plotted against variance of the length, width and breadth of the seeds of 40 species to give an indication of persistence in soil (adapted from Thompson, 1993a).

An unspecialised dispersal mechanism, when combined with a seed bank, is characteristic of the flora of permanent but unpredictably disturbed habitats (Roberts, 1962; Cohon ,1966; Kropáč, 1966; Cohon ,1967; MacArthur, 1972; Wilcott, 1973; Meredith, 1978; Thompson & Grime, 1979; Venables & Lawlor, 1980; Cavers, 1983; Ritland, 1983; Ellner, 1985a; b; Venables, 1985; Silvertown, 1988; Schulz *et al.*, 1990; Hodgson & Grime, 1990; Putwain & Gillham, 1990; Thompson, 1992; Thompson, 1993b). *L. urens* is suited to such habitats. With a huge potential for recruitment from the seed bank, *L. urens* is able to exploit opportunities for establishment which are widely and unpredictably dispersed in time.

EIGHT

The population matrices
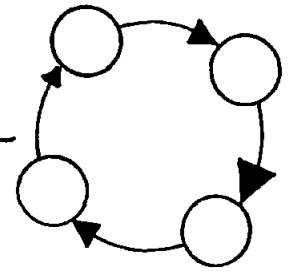
8.1 Introduction

A matrix is a special grouping of numbers designed to manipulate and store large sets of data (Usher, 1972). Entries into a population matrix summarize demographic information on the ways in which survival, growth, development and reproduction change the composition of a population over a given time interval (Begon and Mortimer, 1986). The use of matrix mathematics in models of population behaviour was formalized by Leslie (1945; 1948). The Leslie matrix is an age structured model based on the fecundity and survivorship of discrete age classes in a population. However, size is often a more important determinant of demographic behaviour than chronological age (section 6.1). Lefkovitch (1965) extended the use of matrices to populations classified by stages (instars of insects). The Lefkovitch matrix permits a greater range of transition classes, including changes from larger size classes to smaller ones. For some organisms, such as non-woody perennial plants, this is essential for the development of a realistic matrix (Moloney, 1986). Stage or size classified transition matrices are easily adapted for modelling the population dynamics of plants and have become an increasingly popular tool (van Groenendael *et al.*, 1988). Investigations using stage classed matrices include the demography of annual (Leverich & Levin, 1979), biennial (Werner & Caswell, 1977; Caswell, 1978) and perennial (Sarukhán & Gadgil, 1974; Ehrlén, 1995) herbs, as well as grasses (Law, 1983; Mack & Pyke, 1983; Moloney, 1988) and trees (Maillette, 1982; Piñero *et al.*, 1984; Huenneke & Marks, 1987). Caswell (1982; 1985) adapted matrix methods to the demography of organisms with complex life cycles, including those capable of both sexual and clonal reproduction. His methods have since been used in a number of studies including that of the clonal shrub *Alnus incada* ssp. *rugusa* (Huenneke & Marks, 1987) and *Arisaema triphyllum*, a herbaceous perennial that changes sex (Bierzychudek, 1982).

Transition matrix models have been used in the conservation of rare or endangered species such as that of loggerhead turtles (*Caretta caretta*) (Crouse *et al.*, 1987), *Widderingtonia cedarbergensis* (Manders, 1987) and Mariposa lilies (*Calochortus*)(Fiedler, 1987). Matrices also play a very important role in management (Bradshaw & Doody, 1978; Zeedyk *et al.*, 1978; Davy & Jefferies, 1981; Charron & Gagnon, 1991; Burgman *et al.*, 1993; Ehrlén, 1995) and are often used to determine species life history aspects that play a key role in the regulation of population numbers (Usher, 1972; Caswell, 1978; Vandermeer, 1978). Complex studies on the variation in matrix transitions with micro-habitat (Hubbell & Werner, 1979) and with disturbance regimes (van Groenendael & Slim, 1988) have been undertaken. Through the comparison of such matrices for different populations or management treatments, suggestions can be made for appropriate management strategies, with the aim of overcoming the constraints on population size (Usher, 1972; Menges, 1986; Manders, 1987).

The previous seven chapters provided information on the ecology of *L. urens* in Britain. A study of the historical ecology of the species, along with its associated plant communities and principal relationships with environmental variables was undertaken in chapter two. Chapters three to six described a four-year study of the demography of *L. urens* within two populations in southwest England. Chapters four and five included details of the number of seedlings emerging, their rates of growth and probability of survival. These three characters were found to vary with the micro-habitat in which seedlings emerged. The presence or absence of moss, litter and depressions at the soil surface and the size of the opening in the established vegetation were investigated. The structure of the two populations and the effects of plant age and size on survival and fecundity were examined as part of chapter six. The variation in the life history characteristics of *L. urens* between and within the two sites were considered throughout. The population response to grazing intensity and frequency at the two sites were compared to ungrazed control plots. Experiments were carried out to support this demographic study. Control laboratory studies explored the dormancy and after-ripening requirements of seeds along with the effects of the light, temperature and moisture environment on germination. The

response of the seed recruitment phase to soil surface micro-habitat, waterlogging and frosting was investigated in glasshouse experiments. Garden studies revealed the development and structure of the rhizome and field experiments looked at the persistence of seed in the soil, the size of the seed bank and the response of adult plant size to intensity of defoliation. All of this information on the demographic characters of *L. urens* is brought together in this chapter to construct population matrices.

Data from chapter six showed size to be more important than age in the determination of the demographic behaviour of *L. urens* (section 6.1 & Tables 6.5, 6.6, 6.10, 6.11) and that the rate of clonal growth can not be ascertained without disturbing the plants (section 6.3.1). In the light of these two observations, a basic Lefkovitch matrix was adopted to address the following questions:

(i) Were the populations stable, expanding or declining?;

(ii) which characters of the life history had most effect on the population growth rate (λ)?;

(iii) what effect did grazing have on the population demography?

Answers to such questions may provide the knowledge necessary for the effective conservation of this plant in Britain.

8.2 Methods

8.2.1 *Determination of size classes*

Development of a classification scheme for assigning individuals to size categories when the character shows continuous variation within a population was not easy (Moloney, 1986). Individuals within the populations had to be classified according to characteristics important to the model, with similar plants being classed together. The analysis of more than one hundred plant species showed consistently recognisable biological stages: seed, seedling, infant, juvenile, virginal, reproductive and senile (Gatsuk *et al.*, 1980). The majority of these stages were

recognised in *L. urens*. However, juvenile and virginal stages were not separated for this matrix as the resultant classes would have been very small (<10). The senile phase of *L. urens* was omitted, as it was indistinct (section 6.1). The selection of the size class limits can cause two sources of error in the transition probabilities (Vandermeer, 1978; Moloney, 1986; Manders, 1987). The first involves the error of estimation (sample error), which occurs in categories that are too small and contain too few individuals. However, a balance must be struck, since the second source arises from the matrix's assumption that individuals within each category are identical (Vandermeer, 1978; Moloney, 1986). Thus, as a category increases in size, the variation between individuals within it also amplifies. Mathematical techniques for equating these two sources of error have been suggested (Vandermeer, 1978; Moloney, 1986), however, in this study, whilst still taking due consideration for the causes of error, a less formal approach was adopted. The survival curves of immature individuals (Figure 5.1) were used in conjunction with growth curves (Figure 5.3) to make subjective selections of the leaf length classes, within which survival chances were similar, and to identify changes in leaf length class, which were associated with an improvement in survival. Similarly, morphological indicators of change in survival and fecundity were used to denote adult classes.

Seed bank estimates

(i) From fecundity estimates

The number of seeds made available to the bank was estimated using the density and fecundity of adult plants. Analysis of variance showed no significant change in total plant density at Andrew's Wood and Redlake between the years 1992 to 1995 (P>0.05, Table 6.2), nor in the number of seeds produced per plant in Andrew's Wood 1993 or 1994 or Redlake in 1994 (P>0.05, Table 8.1). However, significant variation in the density of plants among the seven compartments/grazing treatments (Redlake and Andrew's Wood compartments C and D (grazed, ungrazed and recently cleared) and A8 (P<0.001, Table 6.2 & Figure 6.2)) suggested spatial variation in the number of seeds made available to the seed bank. Insufficient data were collected to analyze for this among the individual compartments of Andrew's Wood (section

6.3.2) but the seeds made available to the bank at Redlake and Andrew's Wood were assessed

separately for the purposes of the transition matrix.

	d.f.	MS	F
Number of seeds per plant	2	133020000.00	1.26

Table 8.1: Results of a one-way ANOVA between the number of seeds per *L. urens* plant at Andrew's Wood (AW) in 1993 and 1994 and at Redlake (RL) in 1994.

The average number of seeds per plant, 1993-1994 was	AW & RL =	6749
and the average number of plants per square metre in 1993-1994	AW =	4.73
	RL =	1.28
therefore, seed production per square metre in 1993-1994 was	AW =	31923
	RL =	8639

These figures were adjusted for a viability of 50% (Figure 4.4), and the resulting estimates of seeds made available to seed bank per metre^2 in 1993-1994 (to the nearest 100) were

AW =	16000
RL =	4300

(ii) From seed bank study

The size of the seed bank within compartment D of Andrew's Wood was estimated to be 17537

seeds in the top 10 cm of soil per m^2 in 1993 (Table 7.1). This was very similar to estimates of

seeds made available to the seed bank 1993-4 (*i* above). The number of seeds in the bank was

expected to be much larger than the annual input as the seed of *L. urens* is long-lived in the soil

(section 7.3) and it is not clear why these two estimates are so close. The seed bank samples

were collected in spring and incubated for 41 days thus reducing error through dormancy

(Raynal & Bazzaz, 1973; Leck & Graveline, 1979) and also catching seed before the

germination peak in May-July (Warr *et al.*, 1993).

From a combination of these two estimates, the final evaluations of the seed bank were taken to

be 16000 seed m^{-2} at Andrew's Wood and 4300 seed m^{-2} at Redlake.

As no germinable seed was detected in the soil of past *L. urens* sites (section 7.2), estimate of losses from seed bank had to be academic. Although this was of potential concern, all evidence pointed towards long-term persistence (section 7.3). An annual loss of 10% was chosen, as this would approximate a half-life of seven years and Thompson (1993a) defined seeds remaining in the soil for more than five years as long-term persistent, while historic evidence suggested *L. urens* to be much longer lived than this (section 2.2). The matrix transitions associated with the seed bank are so large in comparison to the numbers moving in and out of other classes that there is a reasonable margin for error.

Immature period

The immature period covers the vegetative states of *L. urens* from emergence to flowering, hence classification of individuals to within this period was straightforward. The length of the immature period in herbaceous perennials is very variable (Hutchings, 1986) and *L. urens* may flower in its first or second year (section 6.3.2). Those plants which flowered in their first year had a similar survival rate to all flowering individuals, thus, *L. urens* plants were classified as adults from the time of first flowering (section 5.4).

Within the immature period of *L. urens*, three classes were recognised: seedling, infant and juvenile. Classes were identified by the average length of the leaf lamina (leaf length section 6.2.2). Plants were classified as seedlings, from emergence until their first true leaf reached a length of 2 mm. Plants with an average leaf length of between 2 and 9 mm were placed in the infant class and once the average leaf length was more than 9 mm, they moved into the juvenile class. The classes were arbitrarily selected without mathematical procedures, but were chosen by comparing improvement of survival chances of individuals over time (Figure 5.1) and their size (Figure 5.3) and taking due consideration of the two sources of error outlined in section 8.1. The first class was restricted to a relatively small size range, as a large proportion of the losses occurred at this early stage.

Within each of these three classes were two further sub-classes characterised by time of emergence: March-July = early cohort and August-February = late cohort. Timing of emergence had a profound effect on the survival of *L. urens* seedlings (section 5.3). A number of other demographic studies have demonstrated differences in the behaviour of individuals which initiated growth at different times of the year (section 6.4).

Adult period

Rosette and branch number, two independent measures of morphology (Table 6.9), were most important for survival and fecundity of *L. urens*. Both number of rosettes and change in this number were correlated with survival (Tables 6.5 & 6.6). However, a count can be obtained in a single census and, therefore, is of more practical value than a transition, which requires at least two censuses to determine. Plants with more than one rosette had increased chances of survival across both Andrew's Wood and Redlake (Table 6.5). Branch number was correlated with both the number of capsules per plant and the average number of seeds per capsule at Andrew's Wood in 1993 and 1994 but no morphological characteristics were correlated with these measures of fecundity at Redlake (Table 6.10). Branch number was not recorded as part of the annual census, thus, spike height was the only measure of inflorescence size available for this data set (section 3.3). Spike height was also independent of rosette number (Table 6.9) and was not a mere elongation response to sward height. Spike height was not significantly correlated with sward height across Andrew's Wood and Redlake (Spearman rank correlation coefficient 0.55, $P > 0.05$). However, there was some indirect association between sward height and spike height as shown by the relationship among compartments (Figure 8.1). The outliers were compartments A8, where plants had high spikes despite a low mean sward height, and the ungrazed quadrats of compartment C, where, although the sward was high in 1994, the spikes were short. There were no plants in ungrazed quadrats of compartment in 1995. Therefore, it is likely that in 1994 these plants were struggling. The relationship between the remaining four points reflected grazing management. The grazed areas of compartments D and C had both short swards and spikes while those at Redlake and the ungrazed quadrats of compartment D

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were both long.
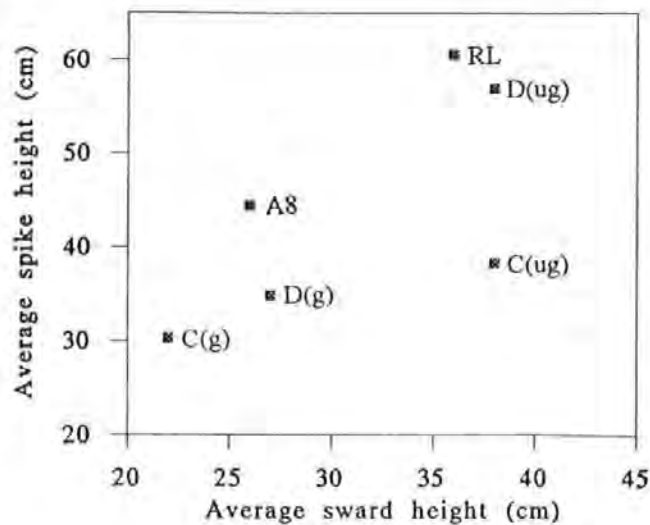
Figure 8.1: Relationship between the average height of *L. urens* flowering spike with sward height in compartments D, C (grazed (g) and ungrazed (ug)) and A8 of Andrew's Wood and at Redlake (RL) in 1994.

Spike height was a true measure of reproductive effort, correlated with the number of capsules per plant, but not with the average number of seeds per capsule (Table 6.10). Adults were assigned to two classes: those with an average flowering spike less than 50 cm and those which were equal to and greater than 50 cm (Figure 8.2). This classification was more satisfactory in 1994 than in 1993. In both years, tall plants were generally variable but plants with flowering spikes of less than 50 cm produced fewer capsules (Figure 8.2). The average fecundity of two classes at both Andrew's Wood and Redlake were estimated (Table 8.2).
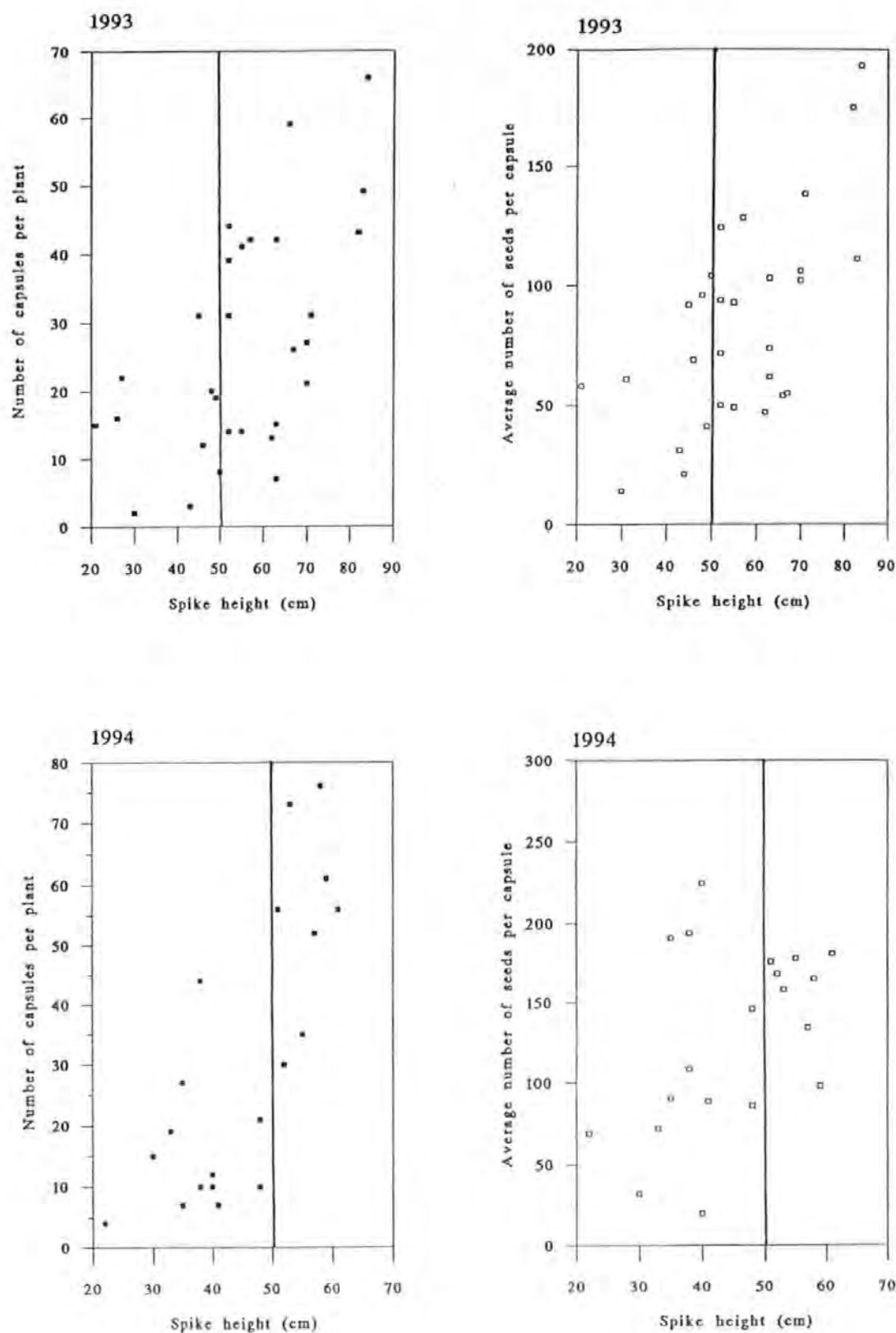
Figure 8.2: Change in fecundity with height of flowering spike at Andrew's Wood in 1993 and 1994.

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Site/year	Fecundity character	Spike height (cm)	
		< 50	≥ 50
Andrew's Wood 1993	Capsules/plant	27±6	84±36
	Seeds/capsule	68±12	94±9
	Seeds/plant	1836	7896
Andrew's Wood 1994	Capsules/plant	20±5	52±6
	Seeds/capsule	114±18	157±12
	Seeds/plant	2280	8164
Redlake, 1994	Capsules/plant	18±0	37±6
	Seeds/capsule	15±0	155±24
	Seeds/plant	270	5735
Rough estimate for fecundity of Andrew's Wood (adjusted for 50% viability)		1000 seeds/plant	4000 seeds/plant
Rough estimate for fecundity of Redlake (adjusted for 50% viability)		150 seeds/plant	3000 seeds/plant

Table 8.2: The average number of capsules per plant and seeds per capsule were used to determine rough estimates for fecundity of short (< 50cm) and tall (≥ 50cm) *L. urens* plants at both Redlake and Andrew's Wood, 1993 and 1994.

The separation of adult plants in terms of fecundity was the most arbitrary dichotomy in the *L. urens* population matrix. Nevertheless, a 50 cm spike height limit (i) divided plants with low fecundity from those with the potential for a higher seed yield and (ii) gave similar numbers of individuals in each class. The probability of an adult producing seed was so high compared to the probability of moving to another adult class that such error in the fecundity calculations was considered to be of little real importance.

Summary of classes

In all there were eleven size classes (Table 8.3).

Class	Abbreviation	Definition
Seed	S	Seed
Early seedling	$Sdl_{(e)}$	Plant, which emerged between March and July, whose first true leaf is still <2 mm
Late seedling	$Sdl_{(l)}$	Plant, which emerged between August and February, whose first true leaf is still <2 mm
Early infant	$I_{(e)}$	Plant, which emerged between March and July, with an average leaf length of 2-9 mm
Late infant	$I_{(l)}$	Plant, which emerged between August and February, with an average leaf length of 2-9 mm
Early juvenile	$J_{(e)}$	Plant, which emerged between March and July, with an average leaf length >9 mm
Late juvenile	$J_{(l)}$	Plant, which emerged between August and February, with an average leaf length >9 mm
Adult one	A1	1 rosette and spike height < 50 cm
Adult two	A2	1 rosette and spike height ≥ 50 cm
Adult three	A3	> 1 rosette and spike height < 50 cm
Adult four	A4	> 1 rosette and spike height ≥ 50 cm

Table 8.3: Summary of the eleven matrix size classes for *L. urens.*

8.2.2 *Construction of transition matrices*

A transition matrix should be constructed from data obtained over fixed discrete intervals of time (Manders, 1987). However, in this study, matrices had to be constructed using overlapping periods, since data from both the annual census of adult plants and the fortnightly detailed census of immature plants were combined. The adult census was undertaken annually from 1992-1995 and transitions covered periods from July to July, while the fortnightly census of immature individuals covered 21 months from March 1993 to February 1995 (Figure 8.3).

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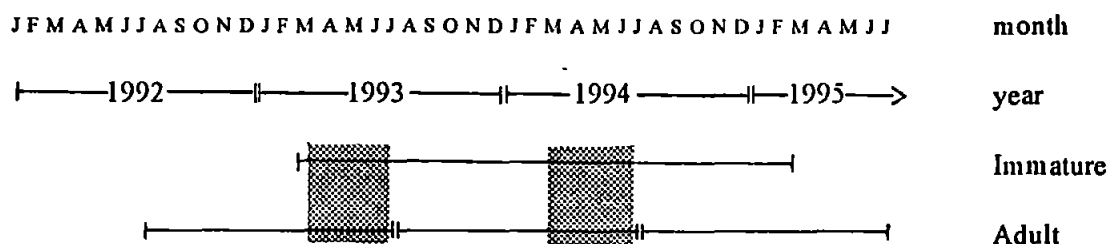
Figure 8.3: Explanatory sketch showing overlapping transition periods of adult and immature censuses. Shaded area denotes most important census period.

The daytime temperatures in southwest England during January and February are well below the minimum temperature for the germination of *L. urens* (section 4.3), so it was not important that the immature census did not begin until March 1993. The adult census had to be carried out in the summer to measure flowering performance. However, the immature census was only carried out March 1993 to February 1995 and therefore the matrix had to be made using overlapping data. It was most important for the matrix that the period March to July was common between the two censuses (Figure 8.3), since this was the important germination and establishment period for *L. urens* at both Redlake and Andrew's Wood (section 4.3). Individuals germinating within the period August to February made no contribution to the population dynamics (section 8.3). Hence, the 1993 transition matrix was constructed of data from the July 1992 to July 1993 adult transitions, combined with the March 1993 to February 1994 seedling transitions, whilst the 1994 transition was constructed of data from July 1993 to July 1994 adult transitions and the March 1994 to February 1995 seedling transitions.

The life cycle of *L. urens* over each calender year was described by a life cycle graph (Hubbell & Werner, 1979) (Figure 8.4). From this graph, a transition count matrix was derived that identified the number of censused plants of each class which stayed in the same class, moved to other classes, or died (Caswell, 1989) (Table 8.4). The immature census covered an area of 5 m^2, whilst the adult census area was 10 times larger. Hence, adult counts were divided by 10 to make the number in the transition count matrix comparable. Transition probabilities were then estimated as the proportion of plants moving between or staying within each of the size classes (Table 8.5).

The diagonal elements represent the probability that a plant remained in the same size class from one year to the next. Neither early seedling nor early infant classes did this but 6.6% of early juvenile plants remained static and flowered the following year. The probability of growth between consecutive size classes is represented by those entries directly below the diagonal in the adult section of the matrix and, because of the early and late sub-classes, by the entry two elements below the diagonal in the immature section. Most movement in the immature section was between consecutive size classes but it was possible for seedlings and infants to move through two or three classes in a single year (Table 8.5), although, of course, it was not possible to move between early and late sub-classes. Adults moved freely between any of the four classes in a year, but the majority of individuals were static or moved only a single class (Table 8.5). The fecundity of each size class was described in the first row of the matrix; that is, transitions from established individuals to seed recruits.

Thirteen matrices were produced in all: one representing the whole of Andrew's Wood in 1993 and one in 1994, and within the reserve for each of these two years, one for compartment D and C (both grazed and ungrazed components separately) and for A8. There was only one matrix for Redlake, which represented the population transitions in 1994, the only year in which immature plants were censused there.

Understanding of all aspects of matrix algebra is not necessary to show how transition matrices are constructed, but it is vital that the basic concepts are clearly understood. A matrix is simply a group of numbers arranged in columns and rows. In transitional studies, the population structure at any given time, when organised into the defined size classes, is written as a single column matrix. The number of elements depends on the number of classes, the matrix for *L. urens* had eleven classes, thus at the beginning of 1993 the population structure (N) could be written:
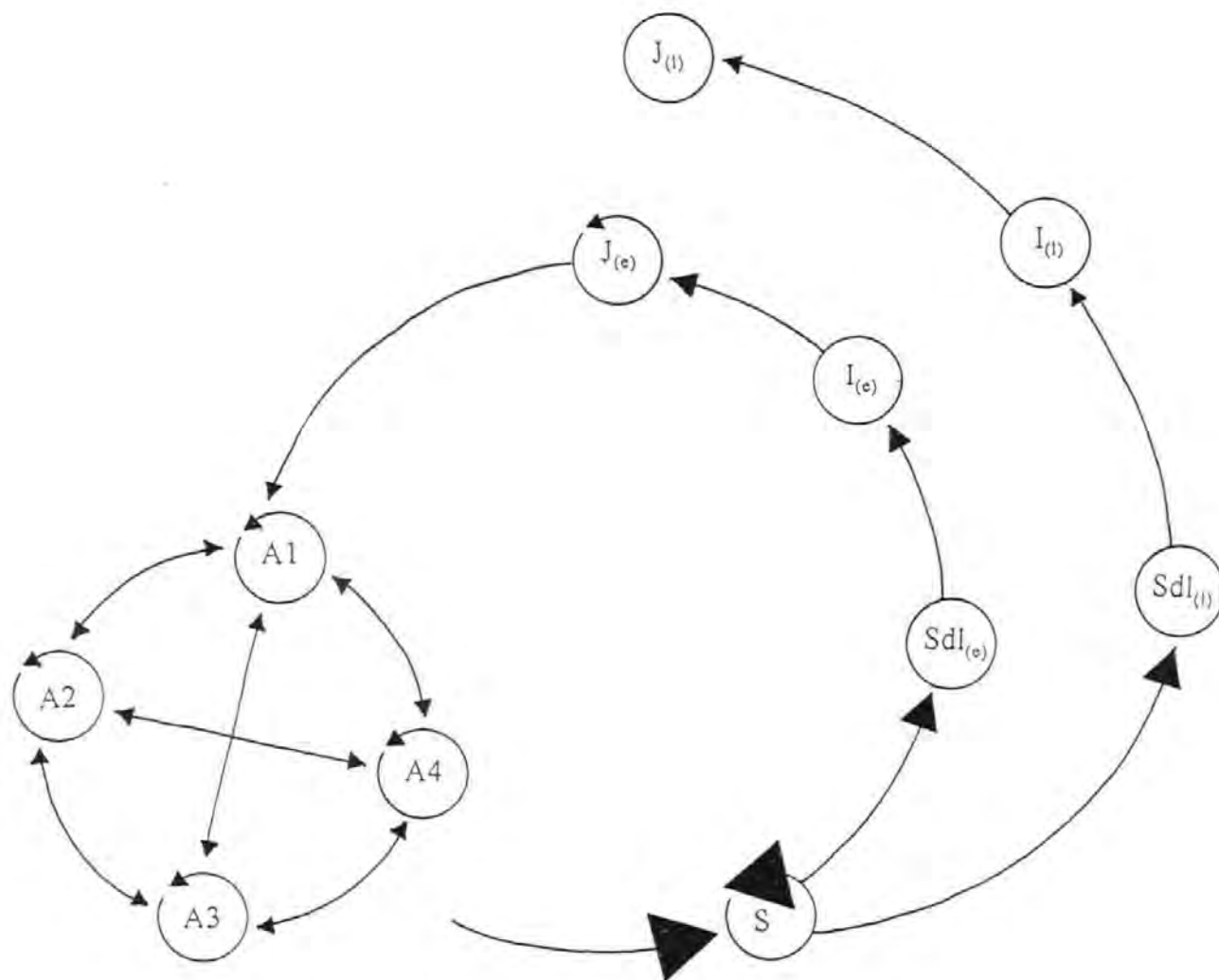
Figure 8.4: Life cycle graph where size of arrow head denotes number of plants making each transition at Andrew's Wood, 1993 (S = seed, Sdl = seedling, I = infant, J = juvenile, (e) = early, (l) = late; for further explanation see Table 8.3).

	S	Sdl$_{(e)}$	Sdl$_{(j)}$	I$_{(e)}$	I$_{(j)}$	J$_{(e)}$	J$_{(j)}$	A1	A2	A3	A4
S	359288							1000	4000	1000	4000
Sdl$_{(e)}$	266										
Sdl$_{(j)}$	133										
I$_{(e)}$	118	73									
I$_{(j)}$	106		74								
J$_{(e)}$	45	38		38		3					
J$_{(j)}$	32		32		32						
A1	10	7		7		7		2	1	3	1
A2	0							2	1	1	6
A3	0							1	1	3	6
A4	0							11	1	3	11
Die	40000	148	27	73	74	35	32	11	6	9	27
Total	400000	266	133	118	106	45	32	17	10	18	51

Table 8.4: Transition count matrix for Andrew's Wood, 1993, from *immature census*, **adult census** and fecundity census/seed bank study.

	S	$Sdl_{(e)}$	$Sdl_{(l)}$	$I_{(n)}$	$I_{(t)}$	$J_{(e)}$	$J_{(l)}$	A1	A2	A3	A4
S	0.89823							1000.0	4000.0	1000.0	4000.0
$Sdl_{(e)}$	0.00066										
$Sdl_{(l)}$	0.00033										
$I_{(e)}$	0.00029	0.27444									
$I_{(l)}$	0.00027		0.55639								
$J_{(e)}$	0.00013	0.14286		0.32203		0.06667					
$J_{(l)}$	0.00008		0.24060		0.30189						
A1	0.00003	0.02632		0.05932		0.15556		0.12139	0.05882	0.14365	0.01961
A2								0.12717	0.13725	0.05525	0.11765
A3								0.04046	0.10784	0.15470	0.11765
A4								0.06936	0.13725	0.16022	0.21569
Die	0.10000	0.55638	0.20301	0.61865	0.69811	0.77777		0.64162	0.55884	0.48618	0.52940

Table 8.5: Transition probability matrix for Andrew's Wood, 1993. Empty cells denote transitions with a zero probability.

$$N_{1993} = \begin{bmatrix} 400000 \\ 266 \\ 133 \\ 118 \\ 106 \\ 45 \\ 32 \\ 17 \\ 10 \\ 18 \\ 5 \end{bmatrix}$$

Matrices with only a single column are called column vectors. Transition matrix, A, can be used to show changes in population numbers (N) from time t to time t+1 by calculating

$$N_{t+1} = AN_t.$$

The multiplication of the initial population structure occurs according to the rules of matrix multiplication (Table 8.6). The population size vector can be iterated (i.e. repeatedly multiplied) by A, and the population eventually stabilizes at a constant ratio of size classes, such that

$$\lambda N = AN$$

where λ (the eigenvalue) denotes population growth rates, such that when $\lambda = 1.0$, the total population size is not changing and $\lambda > 1.0$ indicates population growth, while $\lambda < 1.0$ indicates population decline (Usher, 1972). Matrix algebra can be used to determine a quadratic equation for λ (the eigenvalue) from

$$Ax = \lambda x$$

which yields two possible eigenvalues. Each of these values can be reapplied into the equation to give a corresponding solution to x, these are in the form of column vectors and are called eigenvectors. These solutions are vectors for which multiplication by the matrix (A) is equivalent to multiplication by a single number, the eigenvalue (λ). The right eigenvector is the stable size structure of the population and the left eigenvector, the stable reproductive values for each size class. These are of interest in themselves (Silvertown et al., 1993) but they may also be multiplied together to calculate the sensitivity of each element in the matrix (Caswell, 1978). Each element of the sensitivity matrix is the reproductive value of the size class, weighted by its relative abundance. The sensitivity matrix evaluates the relative importance that different stages

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$$
\begin{vmatrix}
0.89823 & & & & & 1000.0 & 4000.0 & 1000.0 & 4000.0 \\
0.00066 & & & & & & & & \\
0.00033 & & & & & & & & \\
0.00029 & 0.27444 & & & & & & & \\
0.00027 & & 0.55639 & & & & & & \\
0.00013 & 0.14286 & & 0.32203 & & 0.06667 & & & \\
0.00008 & & 0.24060 & & 0.30189 & & & & \\
0.00003 & 0.02632 & & 0.05932 & & 0.15556 & 0.12139 & 0.05882 & 0.14365 & 0.01961 \\
& & & & & & 0.12717 & 0.13725 & 0.05525 & 0.11765 \\
& & & & & & 0.04046 & 0.10784 & 0.15470 & 0.11765 \\
& & & & & & 0.06936 & 0.13725 & 0.16022 & 0.21569
\end{vmatrix}
\times
\begin{vmatrix}
400000 \\
266 \\
133 \\
118 \\
106 \\
45 \\
32 \\
17 \\
10 \\
18 \\
5
\end{vmatrix}
=
$$

$$
\begin{vmatrix}
(0.89823)(400000)+(1000.0)(17)+(4000.0)(10)+(1000.0)(18)+(4000.0)(5) \\
(0.00066)(400000) \\
(0.00033)(400000) \\
(0.00029)(400000)+(0.27444)(266) \\
(0.00027)(400000)+(0.55639)(133) \\
(0.00013)(400000)+(0.14286)(266)+(0.32203)(118)+(0.06667)(45) \\
(0.00008)(400000)+(0.24060)(133)+(0.30189)(106) \\
(0.00003)(400000)+(0.02632)(266)+(0.05932)(118)+(0.15556)(45)+(0.12139)(17)+(0.05882)(10)+(0.14365)(18)+(0.01961)(5) \\
(0.12717)(17)+(0.13725)(10)+(0.05525)(18)+(0.11765)(5) \\
(0.04046)(17)+(0.10784)(10)+(0.15470)(18)+(0.11765)(5) \\
(0.06936)(17)+(0.13725)(10)+(0.16022)(18)+(0.21569)(5)
\end{vmatrix}
=
\begin{vmatrix}
454292 \\
264 \\
132 \\
189 \\
182 \\
131 \\
96 \\
38 \\
5 \\
5 \\
7
\end{vmatrix}
$$

Table 8.6: Multiplication of 1993 population structure vector of *L. urens* at Andrew's Wood by 1993 transition matrix .

have on the finite rate of increase of the population. These sensitivity values can be standardized to allow for the fact that elements representing survival probabilities can only range between zero and one, whereas an element representing fecundity can have any value. Thus, elasticity values (De Kroon *et al.*, 1986), represent the proportional sensitivities. Values for each matrix sum to 1.0, thus allowing comparisons between classes and between matrices as to those elements which are most important to population increase and those which are constraining the population. Furthermore, selected regions of the elasticity matrix may be summed in order to examine the overall impact of, say, fecundity, growth or a particular size class to λ (De Kroon *et al.*, 1986).

When looking for a stable size class distribution to calculate λ and carrying out elasticity analyses, the initial column vector N, is unimportant. Whatever values are in this initial vector, when multiplied by A repeatedly, the resultant vectors will converge to the same stable size class distribution. However, rather than repeatedly multiplying a random vector by the transition matrix until a stable size distribution is reached to yield information on present population status, the column vector representing the number of plants in each a given size class at time t can be multiplied by the transition matrix a known number of times, to predict the state of that population at a given time in the future. This method assumes that the transition matrix remains constant over time.

8.3 Results

Emerging as a seedling late in the year was of no value to λ throughout Andrew's Wood and Redlake (Tables 8.5 & 8.7-8.10). Therefore, it was not important that the period August to December of the immature census was out of synchrony with the adult census (section 8.2.2). Overall, the *L. urens* population at Andrew's Wood was growing throughout 1993 and 1994 (λ = 1.32 & 1.38, Tables 8.7 & 8.8). In 1994, there were no transitions out of the infant class in the population at Redlake (Table 8.10) and therefore the life cycle was not complete, which

meant that the matrix iteration did not reach a stable population distribution and it was not possible to obtain a value for λ or an elasticity matrix.

Elasticity analyses of Andrew's Wood revealed that the seed class had the highest impact on the population making up 40-50% of the total contribution to λ. The majority of this contribution was made by seed staying in the bank (25-40%) but fecundity was also of considerable importance (Tables 8.5 & 8.7-8.9). The first adult class made a larger contribution to the population growth rate (λ) (around 20%, Tables 8.7 & 8.9) than classes two to four, since emergers all moved to this class first. Across Andrew's Wood, *L. urens* was characterised by low elasticities for movement in many of the adult classes in comparison to fecundity, germination and growth through immature classes (Tables 8.5 & 8.7-8.9).

The matrices of Andrew's Wood (Tables 8.5 & 8.7-8.9) provided an overview of the life cycle of the *L. urens* population across the entire reserve but they must be considered with an awareness for the difficulties of understanding an entire species from a single patch or number of patches (Fiedler, 1987). The spatial heterogeneity in demographic rates within the population at Andrew's Wood was considerable. The decline of the sub-population in compartment C was evident from the lack of successful recruitment from seed, even in the grazed areas, combined with a high adult death rate (Tables 8.18 & 8.21). At the same time, the sub-population of A8 was thriving with a growth rate of 1.2-1.4 (Tables 8.22 & 8.24).

The effect of grazing management on the population growth rates of *L. urens* was illustrated by the changing values of the elasticity matrix elements and the resultant λ values. Elasticities for the grazed areas of compartment D were similar in 1993 and 1994 (Tables 8.12 & 8.14). They were characterised by the relatively large contribution to λ made by seed staying in the bank and by the positive transitions between seedlings and the immature classes and from these to the adult class one. The adult transitions made little contribution save stasis in classes one or two or moving up from class one to two. As most adults were within class one, this class made the

largest fecundity contribution (Tables 8.12 & 8.14). In 1993, the ungrazed quadrats of compartment D had similar emphasis on emergence and growth through immature classes as the grazed areas (Table 8.16). However, staying in the juvenile class for a year and flowering the following year was not a feature of the ungrazed population, and stasis in adult classes one, two or three made very little contribution to λ (Table 8.16). Instead, the most important transitions of the ungrazed area were those from any of the adult classes up to adult class four (Table 8.16). In an ungrazed community, adult *L. urens* plants had the ability for rapid growth, skipping a number of classes (Table 8.15). Class four made the largest contribution to λ as a result of the number of individuals moving into the class, combined with the larger fecundity of individuals in this class (Table 8.16). Thus, large plants were very important in the ungrazed community. In the ungrazed area in 1994, as seen at Redlake, no transitions were made out of the immature section, the life cycle was not complete, the matrix iteration did not reach equilibrium and it was not possible to obtain an elasticity matrix (Table 8.17). This was also the case in compartment C of Andrew's Wood (Table 8.18-8.21). In compartment A8, again there was little difference in transitions between the years (Tables 8.22 & 8.24), although there were more individuals in adults classes three and four in 1994 and, as a result, the fecundities of these classes made larger contributions to λ than in 1993 (Tables 8.23 & 8.25). λ was particularly large in A8, 1994 (1.40) and concurrently, seed that stayed in the bank was less important, whilst seed which reached adult class one played a significant role in determining long-term population growth rates (Table 8.23). For both years in A8, moving from adult one to larger adult classes was the most critical part of the life history outside the seed bank but other adult transitions were of considerably less significance (Tables 8.22 & 8.24).

	S	$Sdl_{(e)}$	$Sdl_{(l)}$	$I_{(e)}$	$I_{(l)}$	$J_{(e)}$	$J_{(l)}$	A1	A2	A3	A4	sum
S	0.34952							0.07979	0.04720	0.00432	0.03398	0.51481
$Sdl_{(e)}$	0.05718											0.05718
$Sdl_{(l)}$												
$I_{(e)}$	0.04149	0.01569										0.05718
$I_{(l)}$												
$J_{(e)}$	0.02575	0.01574		0.02169	0.00326							0.06645
$J_{(l)}$												
A1	0.04086	0.02576		0.03550	0.05992			0.01694	0.00097	0.00109	0.00023	0.18127
A2								0.05183	0.00662	0.00122	0.00408	0.06375
A3								0.00659	0.00208	0.00137	0.00163	0.01167
A4								0.02938	0.00688	0.00368	0.00776	0.04770

Table 8.7: Elasticity matrix for *L. urens* at Andrew's Wood, 1993. $\lambda = 1.32$.

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	S	$Sdl_{(e)}$	$Sdl_{(l)}$	$I_{(e)}$	$I_{(l)}$	$J_{(e)}$	$J_{(l)}$	A1	A2	A3	A4
S	0.89764							1000.00	4000.00	1000.00	4000.00
$Sdl_{(e)}$	0.00135										
$Sdl_{(l)}$	0.00037										
$I_{(e)}$	0.00026	0.09630									
$I_{(l)}$	0.00015		0.16326								
$J_{(e)}$	0.00013	0.07778		0.40385							
$J_{(l)}$	0.00008		0.23129		0.58621						
A1	0.00003	0.01852		0.09615	0.19231			0.26667	0.04396	0.10811	0.03125
A2								0.08148	0.20879	0.06757	0.06250
A3								0.05183	0.15385	0.36486	0.10417
A4								0.08148	0.25275	0.16216	0.68750
Die	0.10000	0.80740	0.60545	0.50000	0.41379	0.80769	1.00000	0.51854	0.34065	0.29730	0.11458

Table 8.8: Transition matrix for *L. urens* Andrew's Wood, 1994. $\lambda = 1.38$.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4	sum
S	0.28674							0.06706	0.02772	0.00538	0.05548	0.44238
Sdl$_{(e)}$	0.05240											0.05240
Sdl$_{(l)}$												
I$_{(e)}$	0.03850	0.01390										0.05240
I$_{(l)}$												
J$_{(e)}$	0.02432	0.01418		0.01930								0.05780
J$_{(l)}$												
A1	0.04041	0.02432		0.03310	0.05781			0.03771	0.00051	0.00123	0.00073	0.19582
A2								0.03550	0.00752	0.00236	0.00451	0.04989
A3								0.01026	0.00252	0.00579	0.00341	0.02198
A4								0.04528	0.01161	0.00723	0.06322	0.12734

Table 8.9: Elasticity matrix for *L. urens* Andrew's Wood, 1994.

	S	$Sdl_{(e)}$	$Sdl_{(l)}$	$I_{(e)}$	$I_{(l)}$	$J_{(e)}$	$J_{(l)}$	A1	A2	A3	A4
S	0.89959							150.000	3000.00	150.000	3000.00
$Sdl_{(e)}$	0.00031										
$Sdl_{(l)}$	0.00001										
$I_{(e)}$	0.00009	0.30159									
$I_{(l)}$											
$J_{(e)}$											
$J_{(l)}$											
A1									0.04167		
A2								1.00000	0.08333		0.10526
A3									0.08333		
A4									0.20833		0.57895
Die	0.10000	0.69841	1.00000	1.00000					0.58334	1.00000	0.31579

Table 8.10: Transition matrix for *L. urens* at Redlake, 1994. Not a complete cycle.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.89706							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$	0.00165										
Sdl$_{(l)}$	0.00036										
I$_{(e)}$	0.00060	0.26515									
I$_{(l)}$	0.00007		0.79310								
J$_{(e)}$	0.00016	0.08333		0.22917							
J$_{(l)}$	0.00006		0.17241		0.17857						
A1	0.00002	0.01515		0.04167		0.15385		0.26087	0.13333	0.21429	
A2								0.04348	0.13333	0.02857	0.16667
A3								0.04348	0.26667	0.17143	0.16667
A4										0.01429	
Die	0.10000	0.63637	0.03449	0.72916	0.82143	0.74615	1.00000	0.65217	0.46667	0.57142	0.66667

Table 8.11: Transition matrix for *L. urens* in the grazed area of compartment D Andrew's Wood, 1993, $\lambda = 1.23$.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4	sum
S	0.40859							0.12214	0.02498	0.00626	0.00036	0.56233
Sdl$_{(e)}$	0.06502											0.06502
Sdl$_{(l)}$												
I$_{(e)}$	0.04088	0.02414										0.06502
I$_{(l)}$												
J$_{(e)}$	0.02388	0.01662		0.02644								0.06694
J$_{(l)}$												
A1	0.02396	0.02425		0.03858		0.06695		0.04190	0.00088	0.00176		0.19828
A2								0.02677	0.00336	0.00090	0.00006	0.03109
A3								0.00747	0.00187	0.00151	0.00002	0.01087
A4										0.00044		0.00044

Table 8.12: Elasticity matrix for *L. urens* in the grazed area of compartment D Andrew's Wood, 1993.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.89880							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$	0.00072										
Sdl$_{(l)}$	0.00026										
I$_{(e)}$	0.00022	0.18966									
I$_{(l)}$	0.00007		0.09524								
J$_{(e)}$	0.00009	0.10345		0.33333		0.28571					
J$_{(l)}$	0.00005		0.19048		0.66666						
A1	0.00004	0.01724		0.05556		0.14286		0.31373		0.05263	
A2								0.03922	0.28571	0.02632	
A3								0.23529	0.42857	0.39474	1.00000
A4								0.01961		0.07985	
Die	0.10000	0.68965	0.71428	0.61111	0.33334	0.57143	1.00000	0.39215	0.28572	0.44646	

Table 8.13: Transition matrix for *L. urens* in the grazed area of compartment D Andrew's Wood, 1994. $\lambda = 1.27$.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4	sum
S	0.36848							0.08602	0.02103	0.02881	0.01562	0.51996
Sdl$_{(e)}$	0.04185											0.04185
Sdl$_{(l)}$												
I$_{(e)}$	0.02781	0.01361										0.04142
I$_{(l)}$												
J$_{(e)}$	0.02017	0.01316		0.01930		0.01530						0.06793
J$_{(l)}$												
A1	0.06164	0.01508		0.02212		0.05262		0.05072		0.00285		0.20503
A2								0.02001	0.00713	0.00450		0.03164
A3								0.03907	0.00348	0.02195	0.00603	0.07053
A4								0.00922		0.01243		0.02165

Table 8.14: Elasticity matrix for *L. urens* in the grazed area of compartment D Andrew's Wood, 1994.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.89985							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$	0.00005										
Sdl$_{(l)}$											
I$_{(e)}$	0.00005	0.50000									
I$_{(l)}$											
J$_{(e)}$	0.00002										
J$_{(l)}$											
A1	0.00002	0.50000		0.50000		1.00000		0.06780	0.03704	0.06818	
A2								0.25424	0.11111	0.18182	0.25000
A3								0.05085	0.05555	0.04545	0.10000
A4								0.20339	0.24074	0.54545	0.30000
Die	0.10000			0.50000				0.42372	0.55556	0.15910	0.35000

Table 8.15: Transition matrix for *L. urens* in the ungrazed area of compartment D Andrew's Wood, 1993. $\lambda = 1.37$.

	S	$Sdl_{(e)}$	$Sdl_{(l)}$	$I_{(e)}$	$I_{(l)}$	$J_{(e)}$	$J_{(l)}$	A1	A2	A3	A4	sum
S	0.31537							0.04247	0.05733	0.00304	0.06114	0.47935
$Sdl_{(e)}$	0.05257											0.05257
$Sdl_{(l)}$												
$I_{(e)}$	0.03849	0.01407										0.05256
$I_{(l)}$												
$J_{(e)}$	0.03080											0.03080
$J_{(l)}$												
A1	0.04212	0.03849		0.05257		0.03080		0.00865	0.00128	0.00062		0.17453
A2								0.05914	0.00698	0.00303	0.01674	0.08589
A3								0.00927	0.00273	0.00059	0.00525	0.01784
A4								0.05500	0.01757	0.01056	0.02336	0.10649

Table 8.16: Elasticity matrix for *L. urens* in the ungrazed area of compartment D Andrew's Wood, 1993.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.89977							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$	0.00014										
Sdl$_{(l)}$	0.00005										
I$_{(e)}$											
I$_{(l)}$	0.00002										
J$_{(e)}$					1.00000						
J$_{(l)}$	0.00002										
A1								0.21053			
A2								0.21053	0.21429		0.08333
A3								0.26316	0.07143	0.27273	0.02778
A4								0.26316	0.33929	0.54545	0.80555
Die	0.10000	1.00000	1.00000				1.00000	0.05262	0.37221	0.18182	0.08332

Table 8.17: Transition matrix for *L. urens* in the ungrazed area of compartment D Andrew's Wood, 1994. Not a complete cycle.

	S	$Sdl_{(e)}$	$Sdl_{(l)}$	$I_{(e)}$	$I_{(l)}$	$J_{(e)}$	$J_{(l)}$	A1	A2	A3	A4
S	0.89754							1000.00	4000.00	1000.00	4000.00
$Sdl_{(e)}$	0.00062										
$Sdl_{(l)}$	0.00059										
$I_{(e)}$	0.00029	0.40000									
$I_{(l)}$	0.00044		0.48936								
$J_{(e)}$	0.00037	0.06000		0.13043		0.16667					
$J_{(l)}$	0.00015		0.25532		0.34286						
A1										0.08696	
A2											
A3								0.04545	1.00000	0.30435	
A4											
Die	0.10000	0.54000	0.25532	0.86957	0.65714	0.83333	1.00000	0.95455		0.60869	1.00000

Table 8.18: Transition matrix for *L. urens* in the grazed area of compartment C Andrew's Wood, 1993. Not a complete cycle.

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	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.89849							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$	0.00056										
Sdl$_{(l)}$	0.00034										
I$_{(e)}$	0.00018	0.24444									
I$_{(l)}$	0.00005		0.14815								
J$_{(e)}$	0.00038	0.06667		0.21429							
J$_{(l)}$											
A1											
A2											
A3											
A4											
Die	0.10000	0.68889	0.85185	0.78571		1.00000		0.50000		0.50000	1.00000

Table 8.19: Transition matrix for *L. urens* in the grazed area of compartment C Andrew's Wood, 1994. Not a complete cycle.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.90000							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$											
Sdl$_{(l)}$											
I$_{(e)}$											
I$_{(l)}$											
J$_{(e)}$											
J$_{(l)}$											
A1								0.10000		0.10000	
A2								0.10000			
A3								0.05000	0.33333		
A4										0.20000	
Die	0.10000							0.75000	0.66667	0.70000	

Table 8.20: Transition matrix for *L. urens* in the ungrazed area of compartment C Andrew's Wood, 1993. Not a complete cycle.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.90000							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$											
Sdl$_{(l)}$											
I$_{(e)}$											
I$_{(l)}$											
J$_{(e)}$											
J$_{(l)}$											
A1								0.25000			0.20000
A2											
A3								0.25000			0.80000
A4											
Die	0.10000							0.50000			

Table 8.21: Transition matrix for *L. urens* in the ungrazed area of compartment C Andrew's Wood, 1994. Not a complete cycle.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.89813							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$	0.00068										
Sdl$_{(l)}$	0.00047										
I$_{(e)}$	0.00041	0.23171									
I$_{(l)}$	0.00036		0.35088								
J$_{(e)}$	0.00025	0.30488		0.51020		0.10000					
J$_{(l)}$	0.00012		0.26316		0.34884						
A1	0.00004	0.02439		0.04082		0.06667		0.11539	0.06897	0.14706	0.04000
A2								0.11538	0.20690		
A3									0.06897	0.20588	0.12000
A4									0.03448	0.08823	0.20000
Die	0.00001	0.43902	0.38596	0.44898	0.65116	0.83333	1.00000	0.76911	0.62068	0.55883	0.64000

Table 8.22: Transition matrix for *L. urens* in compartment A8 Andrew's Wood, 1993. $\lambda = 1.22$.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4	sum
S	0.43990							0.09845	0.05607	0.00082	0.00225	0.59749
Sdl$_{(e)}$	0.04474											0.04474
Sdl$_{(l)}$												
I$_{(e)}$	0.03426	0.01079										0.04505
I$_{(l)}$												
J$_{(e)}$	0.02131	0.01449		0.01922		0.00491						0.05993
J$_{(l)}$												
A1	0.05727	0.01947		0.02583		0.05502		0.01660	0.00113	0.00018	0.00003	0.17553
A2								0.06046	0.01235			0.07281
A3									0.00127	0.00028	0.00009	0.00164
A4									0.00199	0.00037	0.00046	0.00282

Table 8.23: Elasticity matrix for *L. urens* in compartment A8 Andrew's Wood, 1993.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4
S	0.89400							1000.00	4000.00	1000.00	4000.00
Sdl$_{(e)}$	0.00079										
Sdl$_{(l)}$	0.00061										
I$_{(e)}$	0.00038	0.07260									
I$_{(l)}$	0.00035		0.18947								
J$_{(e)}$	0.00023	0.09368		0.54794		0.16667					
J$_{(l)}$	0.00013		0.29474		0.60870						
A1	0.00007	0.00468		0.02740		0.04762		0.25424	0.11538	0.24000	0.11765
A2								0.08475	0.19231	0.12000	0.00000
A3								0.10169	0.23077	0.32000	0.17647
A4								0.06780	0.15385	0.12000	0.47059
Die	0.10000	0.82904	0.51579	0.42466	0.39130	0.78571	1.00000	0.46152	0.69231	0.20000	0.23529

Table 8.24: Transition matrix for *L. urens* in compartment A8 Andrew's Wood, 1994. $\lambda = 1.40$.

	S	Sdl$_{(e)}$	Sdl$_{(l)}$	I$_{(e)}$	I$_{(l)}$	J$_{(e)}$	J$_{(l)}$	A1	A2	A3	A4	sum
S	0.30898							0.08405	0.03500	0.01087	0.04365	0.48255
Sdl$_{(e)}$	0.03621											0.03621
Sdl$_{(l)}$												
I$_{(e)}$	0.02784	0.00845										0.03629
I$_{(l)}$												
J$_{(e)}$	0.01777	0.01213		0.01584		0.00620						0.05194
J$_{(l)}$												
A1	0.09175	0.01564		0.02045		0.04573		0.04052	0.00153	0.00495	0.00195	0.22252
A2								0.04012	0.00758	0.00735		0.05505
A3								0.02278	0.00431	0.00928	0.00411	0.04048
A4								0.03505	0.00662	0.00803	0.02527	0.09497

Table 8.25: Elasticity matrix for *L. urens* in compartment A8 Andrew's Wood, 1994.

8.4 Discussion

Germination and establishment were the critical phases of the life history of *L. urens* at Andrew's Wood and Redlake throughout the study period. Many species are known to have a poor establishment rate. For example, of the 10000-20000 *Taraxacum* achenes dispersed per square metre, only 0.5% establish successfully (Hofsten, cited in Sheldon, 1974). The germination and establishment of *L. urens* were consistently poor. In the ungrazed area of compartment D, only two seedlings established from an approximated source of 160000 (0.0013%) and even in the adjacent grazed quadrats where 240 germinated, only eight (0.005%) made it to adulthood. Thus, it was important to look at establishment from seed in detail. However, as *L. urens* is a perennial species, analyses of the adult stage had to encompass annual transitions. Hence the life history phases of *L. urens* were observed at two scales and this resulted in a novel two-tiered population matrix.

Matrix analysis can be used to predict the future of populations (Bierzychudek, 1982; Manders, 1987; Menges, 1992) but a major assumption of such models is that transition rates remain constant year after year. This assumption did not hold true for *L. urens*. The influences of temporal changes in the environment on the transition rates of *L. urens* were less apparent than in studies of some species (Moloney, 1988; Svensson *et al.*, 1993, section 6.4.2) but there were annual variations in the transitions of both immature and adult plants. For example, in the grazed areas of compartment D, more individuals moved from seed to seedling in 1993 than in 1994 and more adults moved from classes one and two to higher classes in 1994 than in 1993 (Tables 8.11 & 8.13). In maintaining constant transitions, the matrix model implies that there are no effects of density on population growth. Ultimately this cannot be true, as populations do not continue to grow at a constant rate unregulated (Waite, 1984). In the light of this unfounded assumption, transition matrix models did not provide realistic projections of the long-term population future of *L. urens*. However, there is no doubt about the general usefulness of matrix models as indicators of current demographic trends, even of plant species with quite complex life histories (Huenneke & Marks, 1987; van Groenendael & Slim, 1988; Charron &

Gagnon, 1991). Large data sets can be condensed and evaluated by the means of a few key demographic parameters that are easily calculated from the model.

A population matrix allows demographic data to be represented in a standard format (Silvertown *et al.*, 1993). Thus, comparisons can be drawn between studies and species. The population growth rates of *L. urens* were above the maximum rates of perennial herbs from stable woodland environments e.g. *Panax quinquefolium*, $\lambda = 1.19$ (Charron & Gagnon, 1991), *Chamaelinum luteum*, $\lambda = 1.06$ (Meagher, 1982) and *Arisaema serratum*, $\lambda = 0.99$ (Kinoshita, 1987). The λ values for *L. urens* were more similar to those of herbaceous species from less stable grassy habitats, however, these have produced extremely variable values of λ: 0.58-1.81 for *Pedicularis furbishiae* (Menges, 1990); 0.28-2.61 for *Dipsacus sylvestris* (Werner & Caswell, 1977) and 0.60-1.43 for *Danthonia sericea* (Moloney, 1988). It would appear that this variability is associated with open habitats and ruderal species.

Reproduction and survival made equivalent contributions to the λ of *L. urens* throughout Andrew's Wood (Tables 8.7 & 8.9). A similar trend was found in some herbaceous perennials (De Kroon *et al.*, 1986) but not in climax-forest species *Arisaema triphyllum* (Biezychudek, 1982) or the tropical savanna grass *Andropogon semiberbis* (Silva *et al.*, 1991) where survival contributed much more. It has been suggested that a relatively high elasticity value for fecundity might be more typical of fugitive species, whilst the emphasis lies on growth and survival for long-lived slow growing plants (Sarukhán & Gadgil, 1974; Caswell, 1986; Silvertown *et al.*, 1993).

L. urens may be essentially a ruderal species that adopts a perennial life cycle in Britain. Life history theory has demonstrated that iteroparity may evolve in response to environmental stress (Cohen, 1966; Ellner, 1985a; b; Venables & Brown, 1988). Annual mortalities were higher for immature classes (0.2-1.0 individual individual[-1]) than for adult classes (0.0-0.65 individual individual[-1], Tables 8.5 & 8.7) but both were extremely variable. Chapter five suggests that this

high juvenile mortality may be specific to populations at the northern limit of *L. urens'* distribution. A similar phenomenon was suggested for the herbaceous forest perennial *Panax quinquefolium* (69-92%) at its northern distribution limit (Charron & Gagnon, 1991). Poor juvenile establishment favours the adoption of a perennial life form (Pavlovic, 1994). Confirmation of this in *L. urens* would require a study of the plant's demography towards the centre of its range.

The large seed bank of *L. urens* dominates its population matrices. Seed dormancy is important to *L. urens*, as recruitment from seed is the life history phase most vulnerable to environmental variability and persistent seed is required to obtain sufficient micro-sites after a period unsuitable for reproduction (Pavlovic, 1994). Adult longevity and seed dormancy are viewed as alternative ways of dealing with environmental uncertainty (Venables & Brown, 1988) and there is often a negative relationship between them (Rees, 1994). With a long term seed bank, *L. urens* can persist through unfavourable times. Thus the requirement for adult longevity would generally be less critical. The coexistence of both dormancy and adult longevity as life history characters in the British populations of *L. urens* may also compensate for poor juvenile establishment.

It is of interest that the compartments of Andrew's Wood whose analyses reached equilibrium were growing at such similar rates, whilst the life cycles of the other sub-populations were incomplete; there were no intermediate declining sub-populations. Although two successive transition matrices can be enough to make preliminary analyses (Menges, 1986), they are inadequate to assess how variable life history parameters are in time (Menges, 1990).

Within Andrew's Wood, sub-populations with incomplete life cycles and sub-populations which are increasing in size coexist. The extent and timing of emergence from seed and the density of plants within each compartment fluctuated separately (Figures 4.8 & 6.1b). The sub-populations of the three compartments may have been functioning as a metapopulation (Levins, 1969;
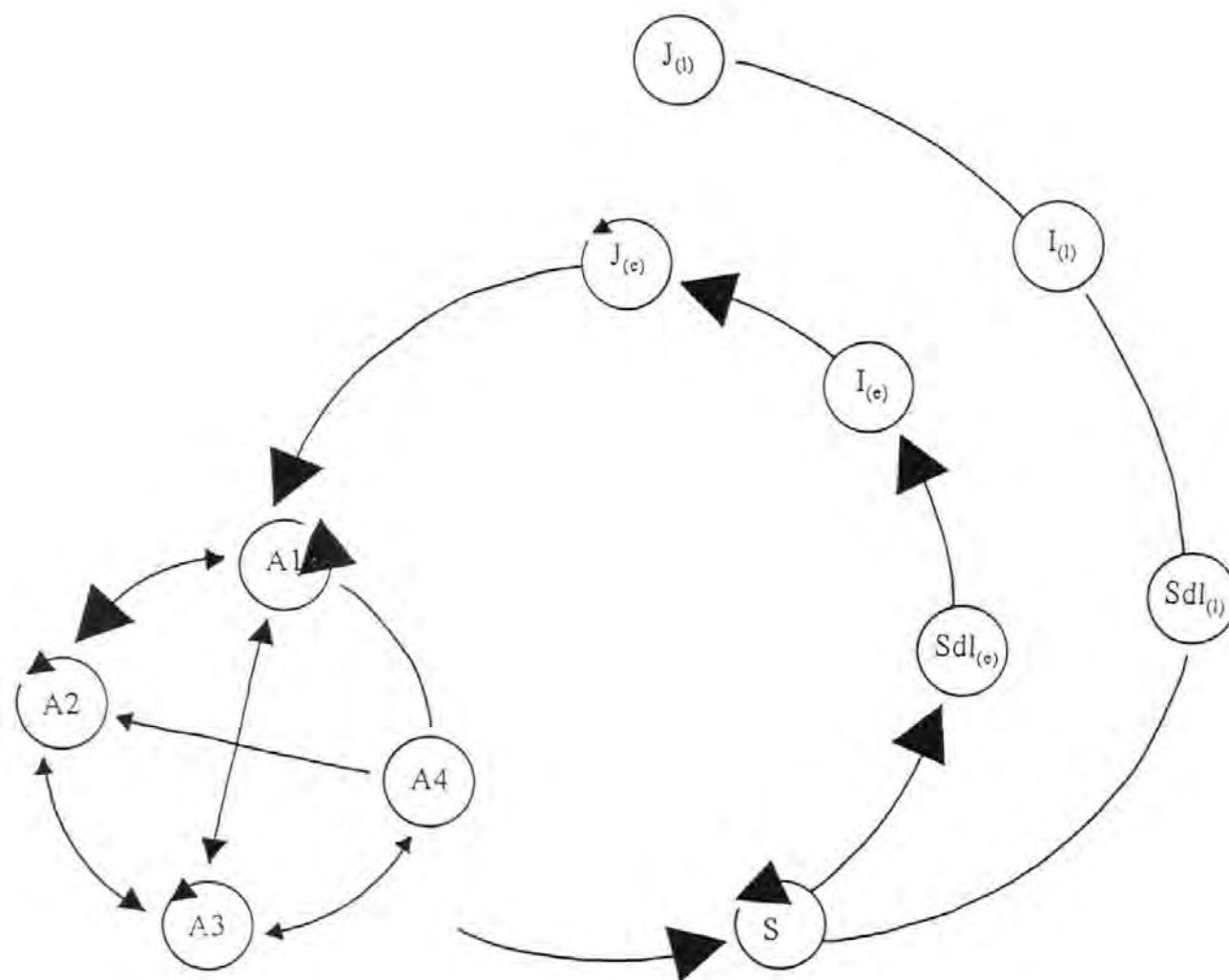
256

Figure 8.5: Life cycle graph showing elasticity of transitions between classes in grazed areas of compartment D, Andrew's Wood. Size of arrow head denotes importance to λ.
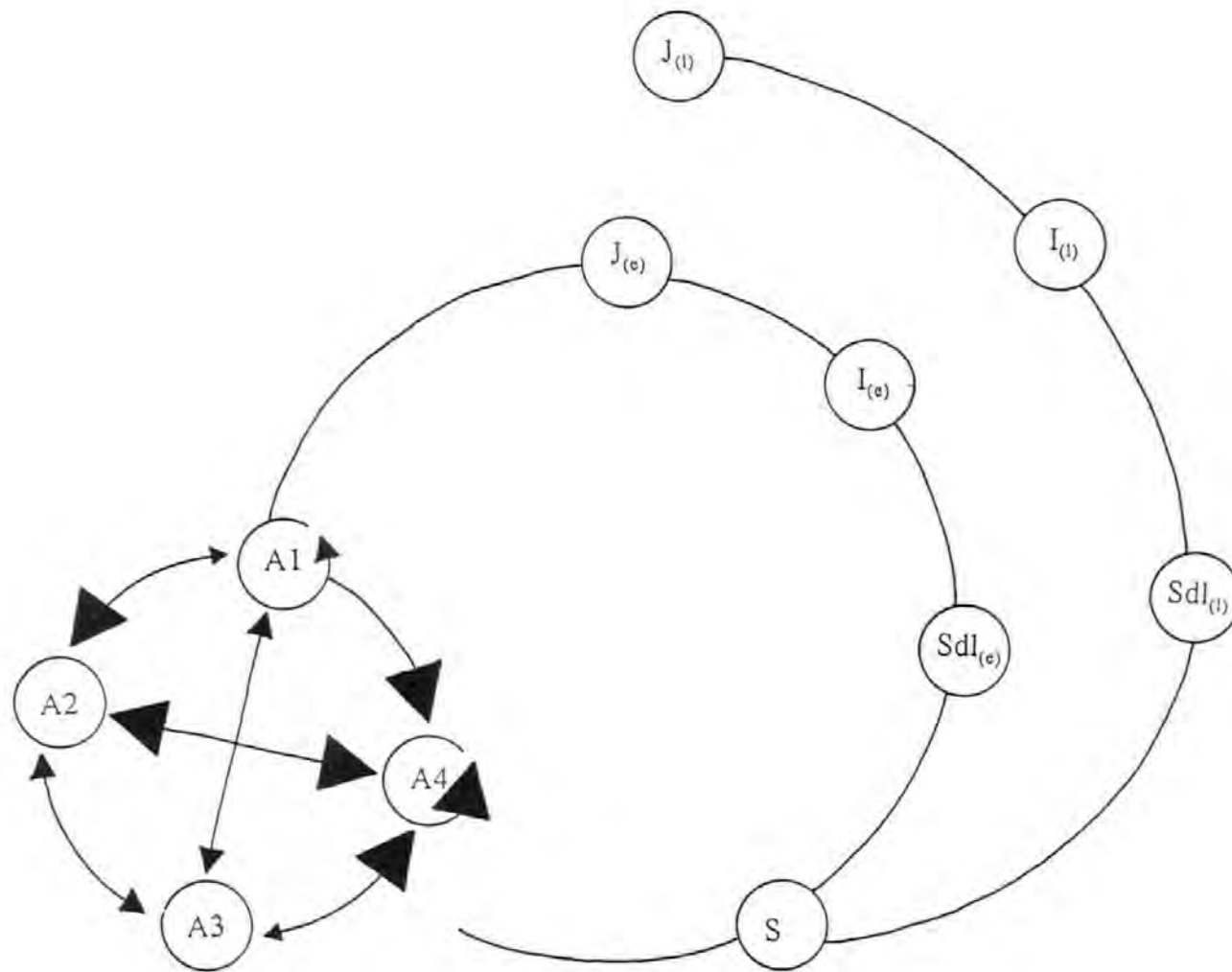
Figure 8.6: Life cycle graph showing elasticity of transitions between classes in ungrazed areas of compartments C & D, Andrew's Wood. Size of arrow head denotes importance to λ.
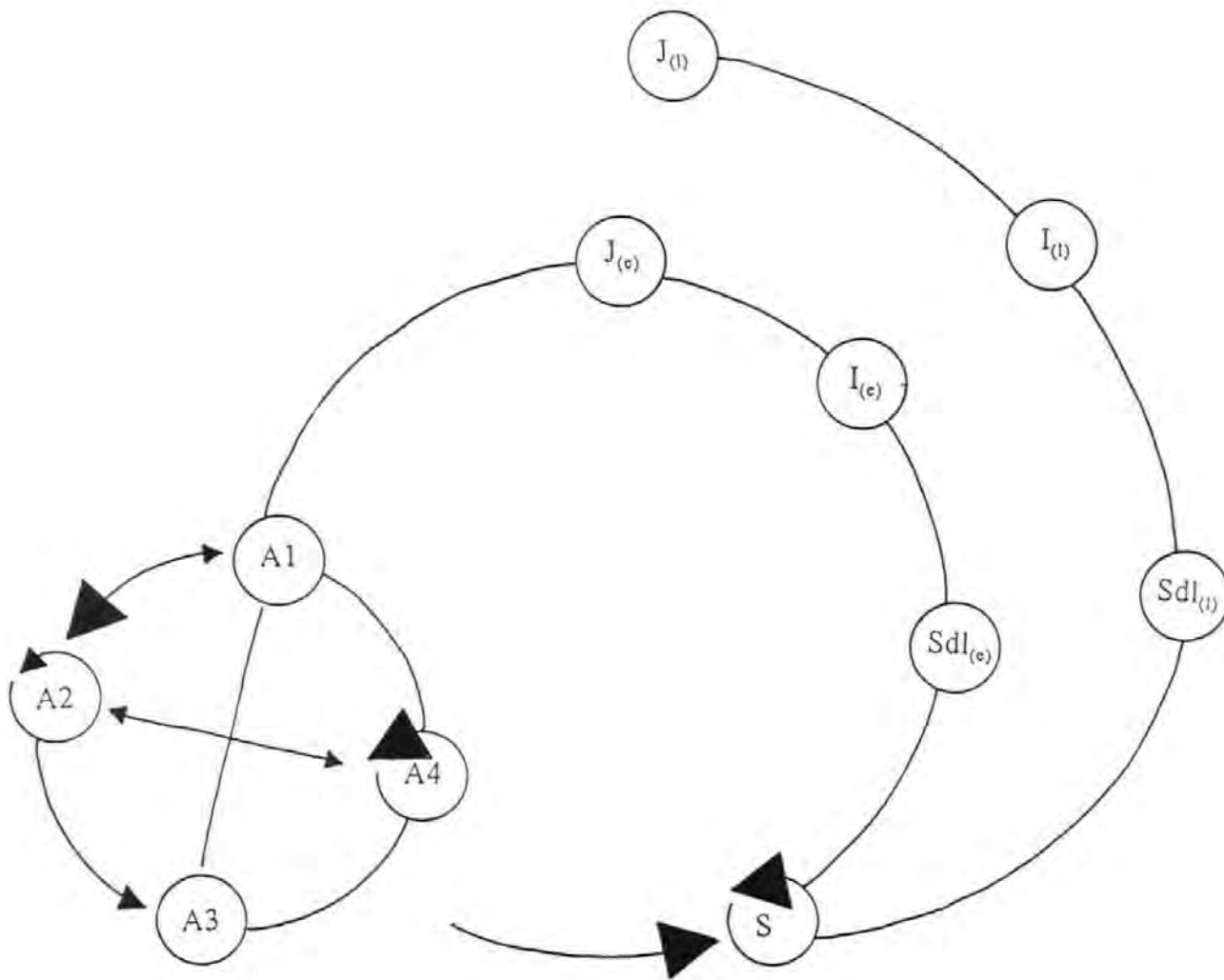
Figure 8.7: Life cycle graph showing elasticity of transitions between classes at Redlake. Size of arrow head denotes importance to λ.

Bleich *et al.*, 1990; see Hanski & Gilpin for a review; Perry & Gonzalez-Andujar, 1993; Doak & Mills, 1994; Hanski & Thomas, 1994). Seed may have dispersed among the compartments, especially between C and D, which were divided by a single line of trees (Figure 3.3). Exchange of seed between C or D and A8 was less likely, as A8 was separated by a substantial expanse of unsuitable habitat (Figure 3.3), although it is improbable that A8 was genetically isolated. The metapopulation affects population persistence through dispersal (Schemske *et al.*, 1994). Over the study period, the sub-population in compartment C was in decline and could have acted as a sink, receiving seed from the fecund plants of compartment D to subsidise the poor performance of its own adults. This theory of the spatial functioning of a metapopulation is less applicable to *L. urens*, due to its high fecundity (irrespective of plant size) and persistent seed bank. The potential for recruitment is dispersed temporally and remains throughout population decline, limited by micro-site availability and not by seed number (sections 4.4 & 5.4).

The population matrices revealed conspicuous differences in the demography of *L. urens* with grazing management (Figures 8.5 - 8.7). The sub-population within the grazed area of compartment D, Andrew's Wood was growing rapidly, whilst the ungrazed areas and Redlake showed incomplete life cycles (Figures 8.5 & 8.7). Although herbivore exclusion increased the size of both the vegetative and reproductive structures of adult plants, which, in turn, improved fecundity and longevity (Figure 8.6; section 6.3), the disturbance of winter grazing was required for regeneration from seed (Figures 8.5 - 8.7). The proportion of adult deaths was similar at both the areas grazed through until spring at Redlake and the winter grazed areas of Andrew's Wood (Tables 8.10, 8.15 & 8.17). Although spring grazing facilitated seedling emergence, it did not bring the benefits to establishment provided by winter grazing (section 6.4.2, Table 8.10 & Figure 8.7).

Population matrices provided a framework for the organisation of data in the research. Information derived from demographic studies, controlled laboratory experiments and garden

studies was brought together in these matrix analyses. The matrices played a descriptive role; rather than modelling future population dynamics, they were used to determine the life history characters important to the regulation of population numbers. The variation in matrix transitions with grazing management was also considered. Such knowledge of the demography and life cycle patterns of a rare species is essential for making informed conservation management descions (Usher, 1972; Menges, 1986; Manders, 1987).
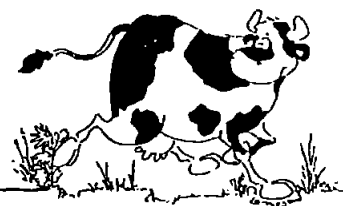
The implications for conservation management

9.1 Difficulties with the design and analysis of demographic studies

Demographic monitoring of plant species is an essential component of effective species

management programmes (Harper, 1977; Davy & Jefferies, 1981; Harvey, 1985; Menges, 1986;

Travis & Sutter, 1986; Hutchings, 1990; Lessica, 1992; Primack, 1993; Given, 1994). Yet

demographic studies yield vast amounts of data, which can be of a complex form and very

difficult to analyse statistically (Owen & Rosentreter, 1992). This research aimed to investigate

the life cycle characteristics of *L. urens*. Careful consideration was given to the logistical and

statistical designs of the experiments and monitoring programmes before the studies began.

However, the data were often less amenable than expected. For example, the emergence of

seedlings was monitored over an area of 25 m^2 for two years and the fate of almost 1000

individuals was followed. This allowed both temporal and spatial comparisons of the numbers

of seedlings emerging. Of those 1000 individuals followed through 1993-1995, nineteen

reached adulthood. Such a low rate of establishment could not have been predicted, but as a

result there were insufficient individuals to compare the probability of survivorship either

temporally or spatially within Andrew's Wood. This made the analyses of survivorship very

difficult, as years and sub-populations had to be combined, despite evidence from precedent

studies of variation in life cycle characters over space and time (Werner & Caswell, 1977;

Bierzychudek, 1982; Piñero *et al.*, 1984; van Groenendael & Slim, 1988; Moloney, 1988;

Charron & Gagnon, 1991; Bullock *et al.*, 1994). A second example of a difficulty with analyses

was experienced with the experimental seed bed, even though the goals of the experiment had

been clearly and concisely outlined and the statistical analyses considered before the study was

initiated (section 4.2.3). The unexpected micro-habitat specificity of *L. urens* produced

binomially distributed data and thus analyses of interactions between the micro-habitat factors

could not be carried out using a nested parametric ANOVA as intended.

Experimental studies need to be designed very carefully if they are to provide the necessary data (Travis & Sutter, 1986; Owen & Rosentreter, 1992). The design of monitoring programmes for rare plants also requires an acute awareness of the problems posed by small population size (Travis & Sutter, 1986). More importantly, despite care with experimental design the data will never be straightforward and a sound statistical knowledge and careful interpretation must always be employed.

9.2 The present status of *L. urens*

L. urens has always been rare in Britain as it is at the edge of its range and is restricted to a narrow band along the south coast of England (section 2.2). Results have suggested that this northern limit to its distribution is enforced by a number of life critical low temperature limits, including the minimum temperature requirements for flowering and seed ripening (section 6.4.2), germination (section 4.4) and establishment (section 5.4). The intolerance of seedlings to frost is at least partly responsible for enforcing the northern distributional limit of *L. urens* (section 4.4). However, the range extends to the Pyrenees and the Spanish Monte de Toledo (section 1.4.1), where winter temperatures are well below those of southern Britain (Pearce & Smith, 1984). The short growing season and low summer temperatures are more likely to combine to limit the establishment and the growth rate at the northern edge of its range. Thus seedlings do not reach the size necessary to withstand the low temperatures of winter and only those seedlings that germinate very early in spring have a chance of survival (section 5.4).

Although *L. urens* in rare in Britain, the highest priority in conservation is given to those species that are rare and endangered throughout all of their geographical range, since they provide particularly important components of the overall genetic diversity of the world's biota (Morse & Henifin, 1981). There has not been a study of the present distribution of *L. urens* in

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continental Europe but the plant is not thought to be endangered at the centre of its range (Daniels, personal communication). The next level of concern is accorded to conservation of sub-species and geographically distinct varieties of plants, since these reflect major aspects of the genetic variation within the species but contribute less to the overall genetic diversity (Morse & Henifin, 1981). The British populations of *L. urens* may well be genetically distinct from Europe; the two have been separated by the North Sea for 8 to 12 000 years (Birks, 1989). Genetically divergent British populations would be of a higher conservation value following the definitions of Morse & Henifin (1981). More importantly perhaps, if *L. urens* is abundant at the centre of its range the species status, or even its extinction in Britain is of little importance.

9.3 The threat of extinction

Conservationists do not aim to increase the abundance and distribution of naturally rare species (Morse & Henifin, 1981), since rarity itself is an endearing quality (Harper, 1981). However, the British populations of *L. urens* are threatened by human activity. The plant occupies the wetlands of lowland agricultural areas, where the pressures of change in land use are greatest (Hodgson, 1986). Successional displacement of the present sites has been rapid; ten indigenous populations have been lost this century, seven of which were a direct result of change in land use (section 2.2).

Whilst habitat loss is certainly the major cause of the modern extinctions, the probability of extinction is accentuated by factors that limit the resilience of populations. Where *L. urens* persists, recruitment is normally low (section 4.3) and is not regulated by the availability of seed (section 7.3): the spatial dispersal of seed locally is adequate and is assisted by temporal dispersal in the seed bank (section 7.3). Instead, the germination of seed is impeded by its high temperature requirement (section 4.4). At the average British spring and summer time temperatures, only 10-20% of the available seeds germinate. Germination is also light-requiring and thus is inhibited by the shade from dead and living plant material (section 4.4). The

establishment phase is also restricted, with less than 3% of the seedlings moving from germination through to adulthood (section 5.3).

The requirements for germination and establishment were rarely met throughout the study and thus these were the major limiting stages of the populations in the South West. Nevertheless, a huge potential for recruitment from the seed bank has been demonstrated in the past (section 2.2). Furthermore, young plants were capable of rapid growth and had a short juvenile period coupled with high fecundity in their first year (sections 5.4 & 6.4.2). These life history characters allowed very rapid increases in the size of *L. urens* populations. Between 1975 and 1976, the population at Andrew's Wood increased by over 2000 plants, and between 1983 and 1984 numbers fell by a similar amplitude (Table 2.1). Stochasticity generally increases the vulnerability of a population to extinction (Schaffer, 1981), yet despite being the cause of these fluctuations in the numbers of *L. urens* plants above ground, the long-term seed bank increases the population's tenacity. A bank of seed acts as a buffer for a population, dampening oscillations of the total population size, that is the size including individuals in the bank, and increases persistence (Kalisz & McPeek, 1992).

L. urens displayed a high level of self-compatibility (section 6.4.2) and this may partly explain the reduced seedling success. The prevalence of self-fertilization in *L. urens* remains unquantified but frequent self-mating can result in genetic uniformity within a population. Populations which lack genetic diversity may experience problems such as low fertility or high mortality among offspring (Lewis, 1979; Charlesworth & Charlesworth, 1987; Kohn, 1988; Hunter, 1996). The theories behind this expression of low fitness include that of heterosis, that heterozygotes are more resistant to disease, grow faster and survive longer than homozygotes (Packer, 1979; Ledig, 1986) and the theory closely linked to evolutionary potential which states heterozgeneous populations are better able to survive in unpredictable environments because of the variation among individuals (Williams, 1966; Allendorf & Leary, 1986).

L. urens is a long-lived species. The adult stages of *L. urens* consist of a number of basal rosettes which form through late autumn to early spring (section 1.1.2). A storage rhizome permits precocious growth early in the season, which is important at the northern limits of its European distribution, where the growing season is shorter. An early start also gives a competitive advantage through the securing of nutrients and water before conspecifics have produced any roots (Svensson *et al.*, 1993). Flowering takes place from June to September and spikes are tall (section 1.1.2). The potential fecundity of *L. urens* was invariably high across compartments and treatments at the two reserves in southwest England (section 6.4.2). Although recruitment requires gaps in the established vegetation, the growth form and phenology allow the adult stages a wider environmental tolerance. Mature plants are able to withstand the dense, high summer swards and encroaching scrub of the associated plant community. The larger plants common in the ungrazed habitats showed improved fecundity and probability of survival (section 6.4).

In addition to the limits of demographic factors on the resilience of populations, the British populations of *L. urens* will be particularly vulnerable if there is little genetic variation within them. This is first because genetic variation is imperative for evolutionary adaptation to a changing environment (Hunter, 1996); second, there are many examples of genetic variation assays on rare and endangered plant populations that show a weak correlation with measures of population size or reproductive success (Fiedler and Jain, 1992). Thus, maintaining population numbers and genetic variation must be a central theme of plans for long-term population management (Lande & Barrowclough, 1987). In Britain, populations of *L. urens* may be prone to a paucity of genetic variation since plant populations whose numbers fluctuate from year to year with short periods of low population numbers, show significantly reduced genetic variation (Crow, 1986). However, recent work has shown the larger populations of Flimwell and Andrew's Wood to be genetically diverse (Daniels, unpublished). The population at Flimwell fell to five plants in 1983 and by 1993 had risen to 2000 plants (Table 2.1). In 1994, there was more diversity in the population than could have originated from five individuals (Daniels,

personal communication). The seed bank embodies a reserve of genetic variability and hence protects that population from the consequences of homozygosity (section 7.1; Gottlieb, 1974; Baskin & Baskin, 1978; Baker, 1989; Levin, 1990; McGraw, 1993)

Integrated monitoring programmes which combine genetic, demographic and experimental investigations for a single rare species are infrequent. Such studies contribute towards a complete understanding of the biology of a rare species and are most useful as a basis for conservation management (Davy & Jefferies, 1981; Lande, 1988). This research has shown that the British populations of *L. urens* have been severely depleted in recent history through change in land use (section 2.2). Populations move rapidly between vigorous growth and unsustaining phases but the seed bank offers protection from stochastic extinction. Hence the probability of the extinction of the remaining populations from demographic or genetic causes is low. Three of the remaining six sites for *L. urens* are managed specifically for nature conservation (section 2.2). The populations here could be stabilized further by the prescription of suitable management to improve the performance of individual plants and influence their probability of entering different life cycle stages.

9.4 Conservation management

At one time, preservation of plants consisted of measures to protect them from physical disturbance, with timber harvests and livestock grazing being excluded and fire suppressed (Hobbs & Huenneke, 1992). An oft quoted example of this practice is that of *Ranunculus ophioglossifolius* at Badgeworth Fen. In 1933, the whole marsh was full of flowering plants and a tall barbed wire fence was erected to protect the plant. For the following thirty years there were virtually no plants within the enclosure (Frost, 1981). Ecologists and conservationists have since come to recognize the need to maintain particular intensities and frequencies of disturbance in areas where it has long been a component of the ecosystem (Platt, 1975; Crawford & Liddle, 1977; Grubb, 1977; Pickett & White, 1985; Klinkhamer & De Jong,

1988; Dolman & Sutherland, 1991; 1992; Hobbs & Huenneke, 1992). Habitat specificity is a common cause of rarity (Harper, 1981; Diamond, 1984; Peters, 1988) and many rare plants require active management in order to stabilize or enlarge protected populations (Connell, 1978; Pickett & White, 1985; Petraitis *et al.*, 1989; Hobbs & Huenneke, 1992; Pavlik & Manning, 1993).

L. urens is rare partly because of its restrictive ecological requirements. Germination and establishment are only reasonably successful following large scale disturbance whilst undisturbed habitats are more favourable for adult plants. Populations of the rhizomatous perennial herb *Hieracium pilosella* also produced larger adult plants and a concomitant reduction in recruitment in ungrazed areas (Bishop *et al.*, 1978). *H. pilosella* populations were prone to extinction on the loss of mature plants through over-grazing, as young plants had a poor reproductive capacity (Bishop *et al.*, 1978). However, *L. urens* populations would be more resilient to this situation, as young plants are capable of rapid growth coupled with high fecundity, even in their first year.

In Britain, *L. urens* is found in habitats which have a history of intermittent soil disturbance (section 2.7) and probably depended upon the natural habitats of woodland clearings caused by fire and wind. The plant exploited the traditional agricultural and forestry practices of rough grazing and coppice, opportunistically, but it is not suited to the intensive management of annual ploughing, drainage, fertilization and improvement (section 2.7). Today, *L. urens* is confined to mesic grasslands which rely on disturbance to control the invasion of trees and shrubs (Smart *et al.*, 1985).

Soil disturbance is as much a traditional part of grass-heath management as coppicing is for many ancient woodlands or haymaking for meadows (Dolman & Sutherland, 1991). Soil disturbance performs numerous functions that facilitate the germination and establishment phases of *L. urens* (sections 4.4 & 5.4), it:

(i) provides gaps in established vegetation and incorporates litter into the soil, both of which improve the light environment at the soil surface;

(ii) creates depressions in the soil surface and promotes the open conditions favoured by moss which help to protect against soil moisture loss;

(iii) brings seed out of the bank. Dormancy in the seed bank is enforced by a requirement for light and not for fluctuating temperatures as in many wetland species. Seed must be brought to the surface to germinate.

Disruption of the soil is still less acceptable than mowing or coppicing and many nature reserves remain overprotected from this management. This research has identified the need for disturbance, but throughout, habitats have been characterised as grazed or ungrazed. This was an obvious oversimplification, which has made it difficult to ascertain the intensity and frequency of disturbance required. One of the most deeply held conservation beliefs is that traditional management should be continued or reinstated wherever possible (Shirt, 1987; Steel & Mills, 1988; Warren, 1993), since the total diversity of native species at the landscape level will be greatest when disturbance occurs at its historic frequency in the historical pattern (Hobbs & Huenneke, 1992). A knowledge of the history of a habitat (section 2.2) lends an insight into the requirements of a community (Dolman & Sutherland, 1991). However, the management chosen should depend on the aims for the site and not solely on tradition (Hambler & Speight, 1995). Often, it is not necessary to mimic the exact historic procedure to achieve similar effects. For example, Breckland heath has been highly disturbed since Neolithic times by shifting ephemeral agriculture, turf stripping and rabbit warrening and these practices were a massive drain on the nutrients of the heath (Dolman & Sutherland, 1991). Dolman & Sutherland (1992) showed how rotovation mimicked the nutrient removal process without reinstating the traditional agricultural practices.

Domestic cattle and horses are often used to maintain species diversity in Europe (Frost, 1981; van Wieren, 1991; Berendse et al., 1992). Mowing is often suggested as an alternative, but it

presents an interesting contrast to grazing management. Although mowing can reduce the growth of competitive dominant grasses, it does not create openings for the recruitment of seedlings as grazing does (Rizand *et al.*, 1989; Sykora *et al.*, 1990; van der Bos & Bakker, 1990). Mowing at Redlake has been accompanied by reapplying the cut vegetation as a mulch later in the year (Cornwall Wildlife Trust 1989 Management Plan, unpublished). This would inhibit the recruitment of *L. urens* from seed. On grass-heath, grazing really is the only viable long-term management option (Dolman & Land, 1995). Furthermore, grazing is much less expensive, especially in rough habitats such as Redlake and Andrew's Wood, where mowing is very labour intensive, as it has to be done with a brush-cutter.

The amount of disturbance inflicted on a community by the grazing animal depends largely upon its identity. Native breeds of moorland ponies (Plate 8.1a) are often available for the grazing of local nature reserves in Devon and Cornwall. Ponies can be very selective grazers. The Exmoor ponies introduced to Redlake in the winter of 1993-4 did not browse the ubiquitous *Betula pubescens* scrub. Hence, the openings created by their trampling were still shaded and re-encroachment of these gaps was rapid. Furthermore, ponies usually repeatedly drop their dung in the same area, causing problems of local nutrient enrichment. These regular dunging areas are also avoided by grazing ponies, with the result that they often develop stands of rank, unpalatable vegetation such as nettles, thistles and ragwort (Ausden & Treweek, 1995). Cattle would be preferred for disturbing the habitats of *L. urens* since they provide heavy trampling and are able to consume coarse vegetation (Spedding, 1971; Dolman & Land, 1995). However, the behaviour of cattle varies to some extent between breeds, and particularly between different ages (Ausden & Treweek, 1995). A herd of mature milking Jerseys (Plate 8.1b) were used to graze Andrew's Wood throughout 1992-1995. These animals are particularly unsuitable since they are both light (section 6.4.1) and sedate, thus providing minimal poaching. Young fattening animals, especially bullocks (Plate 8.1c), are more excitable and therefore provide an increased intensity of trampling. Although the restrictions caused by the availability of graziers, especially to wildlife trusts (Rush & Scott, reserves officers, personal communication)
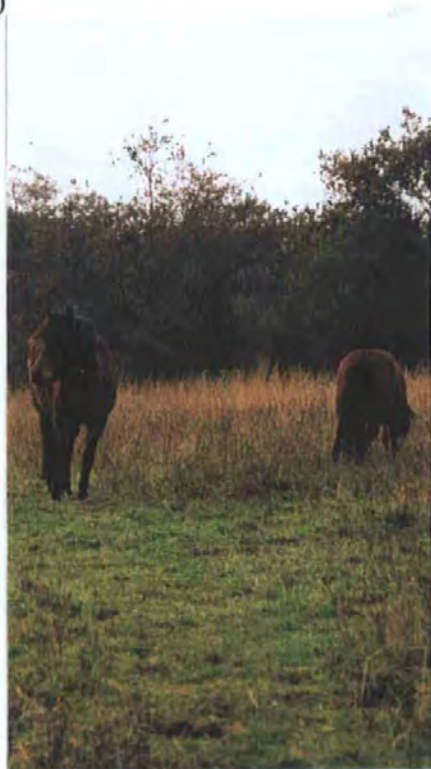
Plate 9.1: Grazing animals (a) Dartmoor ponies, (b) Guernsey milking herd and (c) Friesian bullocks.

is appreciated, every effort must be made to obtain the most suitable animals, since their effectiveness at breaking up the sward is so variable. This may require paying a nominal sum to the grazier to compensate for the poor grazing provided for the animals or, where funds are available, the purchase of specific animals by the managing body.

Despite being the most useful animal, cattle tend to stay in the raised drier areas of wet fields leaving the waterlogged areas significantly less disturbed (personal observation). The suggested method of increasing the intensity of soil disturbance in the wetter communities of Andrew's Wood and Redlake is to force the stock to run around these areas. The pressure exerted on the soil by a galloping cow may reach 0.50 MPa whilst a standing cow creates a pressure in the order of 0.13 MPa (Scholefield & Hall, 1985). This increase in pressure caused by the animal forcing its weight upon a single hoof, greatly increases the amount of soil deformation (Scholefield et al., 1985). An hour of such trampling may result in more soil disturbance than several weeks of conventional stocking.

For rare plants with specialised adaptations to natural disturbance regimes, variation in the scale of disturbance can be critical in determining their population viability (Smart et al., 1985). *L. urens* is well adapted for occasional, but very large scale soil disturbance. Such events recruit dense populations from the buried seed bank and provide large, lasting, open spaces for establishment. They do not need to be frequent, since adult plants are long-lived and able to tolerate dense communities and the buried seed bank is persistent. The most advantageous frequency of the disturbance events will be revealed by the ongoing long-term annual census. However, it is suspected that the populations of *L. urens* will grow most vigorously on a fairly short cycle of three to five years.

The time of year at which disturbance occurs was seen to be important to *Gentiana pneumonathe* because of the increased severity of the effects of fire in drier summer periods (Chapman et al., 1989). Similarly, winter grazing results in most poaching as the ground is

wettest. Winter grazing of cattle is also effective in controlling *Molinia caerulea* as dead litter and rank grass are eaten (Dolman & Land, 1995). To promote the recruitment of *L. urens*, poaching must be of sufficient intensity to maintain open spaces throughout spring as spring grazing is not recommended. Grazing throughout October 1993 to May 1994 at Redlake resulted in the loss of the whole of the spring cohort, as well as a large number of established adults. Spring grazing encouraged the germination of seed too late for the plants to become established before winter.

The importance of a high soil moisture content was suggested through community analyses (section 2.7). Both field and laboratory studies confirmed the recruitment of *L. urens* from seed to be very sensitive to micro-habitat, particularly factors affecting soil moisture status. Emergence was facilitated by the presence of moss and depressions at the soil surface (section 4.3). Experiments showed that germination was little impaired in seeds submerged in water (section 4.3.1) and both field and glasshouse studies showed a significant improvement in establishment with soil waterlogging (section 5.3). The water table of the existing sites of *L. urens* must not be allowed to fall with the drainage of the surrounding agricultural land. The recent management plans of both Redlake and Andrew's Wood have featured the clearance of ditches to improve the drainage. The drains in compartment C of Andrew's Wood and those crossing the fields of Redlake should be filled to raise the soil moisture content. This would assist regeneration in this declining population and sub-population.

This work has provided clear evidence that raising the water table of Redlake and some areas in Andrew's Wood combined with rotational heavy winter grazing would be beneficial to the restoration and conservation of the typical grass-heath on which *L. urens* depends. The spatial heterogeneity of the seed bank must be considered in the management of *L. urens*. A knowledge of the former positions of plants may be necessary to locate the areas where soil disturbance might bring seed out of the bank. Care must be taken, since disturbance presents a conundrum to conservation management by promoting invasibility of communities by non-native

and weedy plant species (Ewel, 1986; Hobbs, 1989 ;1991; Rejmánek, 1989; Hobbs & Huenneke, 1992): for example *Cirsium vulgare* is suited to very similar conditions to *L. urens* (Silvertown & Smith, 1989). However, soil disturbance does not necessarily increase the rate of invasion and some plant communities are more susceptible than others (Hobbs & Atkins, 1988). A primary aim of the management of the wet grassy-heath at both Redlake and Andrew's Wood is to increase the populations of *L. urens*, but the main objective is to conserve the wide range of habitats and biota present at these reserves (unpublished management plans). Recommendations derived from this research for changes in management plans must be confirmed by trial (Harvey, 1985; Burgman *et al.*, 1993; Hambler & Speight, 1995). Morris and Plant (1983) and Ausden & Treweek (1995) both advocate rotational management, which allows disturbance regimes to be tested and provides refuge for those organisms which do not appreciate the prescribed management.

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