VEGETATION DYNAMICS FOLLOWING MANAGEMENT BURNING OF LOWLAND HEATHLAND

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ABSTRACT

Management of the southern lowland heaths is usually for conservation, and aims to create structural diversity, prevent succession to scrub and maintain the low nutrient status of the system. The main aim of this study was to investigate the effects of burning, fire temperature and intensity on seed banks, nutrients, vegetative regeneration and seedling demography.

In the first experiment (1994), vegetation fuel loads were manipulated in stands representing two different growth phases of vegetation (mature and degenerate) at two sites (Arne in Dorset and Aylesbeare in Devon) to test the hypothesis that fire temperature and intensity depend chiefly on fuel load rather than other factors associated with the pre-burn age of the stand. There were two burning treatments of low and high fuel loads. Fire temperatures were measured with temperature-sensitive paints on tiles ('pyrometers'). Intensity (the heat released per unit area) was highly correlated with fuel load. Fire temperatures were higher in the high fuel load treatments than in the low fuel load treatments at all stands except the Aylesbeare degenerate stand, where temperatures were low in both treatments.

In the second experiment (1995), paraffin was added to treatment plots at the mature stand at Aylesbeare in an attempt to produce higher temperatures, but this aim was not achieved. Thermocouples and pyrometers were used to measure temperatures and indicated that these fires were hotter than the fires at the same stand in the first experiment.

There was no effect of burning or of temperature on the size of the seed banks in the soil and litter in the first experiment. The litter seed bank of *Erica tetralix* was depleted by a similar quantity in both treatments in the second experiment. There was no effect of burning on the nutrients (P, Ca, K) in the humic soil in either of the experiments. The concentration of nutrients was higher in the ash than in the litter of control plots after burning (except at the Aylesbeare degenerate stand). There were significant but inconsistent effects of temperature on the quantities of nutrients.

Vegetative regeneration after burning depended chiefly on the pre-burn age of the stand and possibly on grazing, but fire temperature had no effect. There was rapid resprouting at both the mature stands, but regeneration at the degenerate stands was sparse. *Calluna* rapidly regained dominance at the Arne mature stand but was relatively less abundant at the Aylesbeare mature stand after burning than it was before. *Agrostis curtisii*, *Ulex gallii* and *Erica tetralix* were co-dominant in the regrowth at this stand. However, there was a decline in the relative abundances of *U. gallii* and *A. curtisii* by the third growing season after burning.

At the mature stands, seedlings affected by resprouting vegetation were sheltered from microclimatic extremes and experienced higher survivorship than seedlings in areas of bare ground. However, seedling density under resprouts decreased over time as continued growth of resprouts prevented seedling germination and establishment. Seedling populations on bare ground at both types of stand oscillated widely, and there was a rapid turnover. Although bare ground persisted at the degenerate stands, there was no invasion of non-heathland species. A canopy of ericaceous species should eventually develop via gradual accumulation of seedling density and vegetative spread from the few stem bases that were able to resprout.

The range of temperatures generated by the fuel loads tested did not have significant effects on regeneration from seed or from stem bases. However, the removal of vegetation by burning had a large impact on vegetation dynamics by enabling seedling emergence and resprouting from stem bases. The balance between regeneration from seed and from stem bases depended on the pre-burn age of the stand.

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CHAPTER ONE

Introduction

1.1. Heathlands

Heathlands are dominated by dwarf shrubs, principally heather or ling (*Calluna vulgaris* (L.) Hull).[1] They occur throughout the Atlantic zone of north-west Europe on oligotrophic acidic soils. Heathlands are plagioclimax communities and depend on some form of management to prevent invasion of trees. Vegetation dynamics after management fires have been well-studied in Scotland (e.g. Grant, 1968; Hobbs and Gimingham, 1984a and b; Mallik and Gimingham, 1985; Mallik, Hobbs and Rahman, 1988) where burning promotes rapid regeneration from rootstocks, providing young nutritious material for sheep and grouse (Muirburn Working Party, 1977). On the southern lowland heathlands, where habitat conservation is often the priority, management is less concerned with ensuring rapid regeneration and more with creating structural diversity, preventing succession to scrub and maintaining the impoverished nutrient status of the system (Gimingham, 1992). Controlled burning is one of the techniques that can be used to achieve these aims, but has been largely abandoned in the south of England, despite a lack of scientific research on the effects of burning on lowland dry heaths in this area.

Southern heaths have formed on mineral soils, most of which are podsolized due to leaching of bases from the soil profile. They tend to be warmer, drier, more oligotrophic and species-poor than the northern heathlands (Chapman and Clarke, 1980).

1.2. Heather Growth Phases

The life history of *Calluna* has been described by a series of recognisable growth phases (Watt, 1955). The development of seedlings from small pyramid-shaped plants to bushes is known as the pioneer phase. The time spent in this phase is

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[1] *Calluna vulgaris* is referred to as *Calluna* throughout. Nomenclature follows Stace (1997) for vascular plants, Watson (1968) for mosses and Dobson (1992) for lichens.

variable, but tends to be between six and ten years. The building phase is the phase of maximum production (Barclay-Estrup, 1970) and continues until the age of about fifteen years. An even-aged stand of building-phase *Calluna* has a closed canopy and dense shoots. The mature phase lasts for approximately ten years and is recognised by the increasing proportion of woody material and the opening-up of the canopy. After about thirty years, plants enter the degenerate phase, when bushes begin to die off from the centre. The gaps created by dying plants may be colonised by trees, lichens, grasses and bracken *Pteridium aquilinum* (Marrs, 1986), or cyclical succession may take place, whereby *Calluna* establishes from seed (Barclay-Estrup and Gimingham, 1969) or roots adventitiously in the gaps (Gimingham, 1988). After fire, when regeneration is from rootstocks rather than from seed, the pioneer phase may be replaced by a 'post-fire phase', characterised by rapid growth (Chapman and Webb, 1978).

1.3. The Origin of Heathland

In the Atlantic period (7 ka BP), the climate of the British Isles was warmer and wetter than it is today. Tree cover was at a peak, with oak forest in the south and pine forest in the north. Ericaceous species occurred in forest clearings and on exposed coasts and at high altitudes where trees could not establish.

Heathland is thought to have originated primarily from forest clearance by man (Gimingham, 1972; Webb, 1986), starting in the Mesolithic period (12 - 6.5 ka BP). Pollen diagrams from heathland areas show an increase in ericaceous pollen coinciding with a decline in arboreal pollen, indicating the replacement of trees with heathland. The time when this occurred varies greatly between sites but the transition is frequently associated with signs of settlement and cultivation. There is evidence that the poorer soils were deteriorating before man made an impact, but podsolization is thought to have been exacerbated by man (Dimbleby, 1962; Haskins, 1978). The podsolization and deterioration of the soils would have helped prevent the regeneration of trees. Most of the forest clearance occurred in the Bronze Age (3 ka BP), but the appearance of grass, *Plantago* and *Artemisia* pollen as early as the Boreal period (9 ka BP) suggests that Mesolithic man had an impact on the vegetation in some places

(Simmonds and Dimbleby, 1974). The impact of Mesolithic man may have been more pronounced in areas such as Dorset, where soils that originated from poor parent material would have become podsolized more easily (Haskins, 1978).

Neolithic man (4. 5 ka BP) had more impact on the forest cover. This was first described in Denmark by Iversen (1941, 1949; cited in Gimingham, 1972), who found a series of declines in tree pollen and associated increases in ericaceous, cereal and weed pollen. He suggested this was due to a form of shifting agriculture ('landnam'). The forest was often cleared by burning, indicated by a layer of charcoal. The increase in cereal and weed pollen suggests cultivation and then abandonment as the arboreal pollen again increased when the forest re-established.

The 'landnam' phases have also been recognised in the British Isles by Godwin (1956), Mitchell (1951, 1956), and Durno (1965). Grazing by animals during the Neolithic and Bronze Age prevented forest regeneration. The more open landscape that resulted would have accelerated podsolization and heath expansion (Webb, 1986).

A more permanent forest decline began around the beginning of the Iron Age (2.5 ka BP), when ericaceous and agricultural pollen again increased. Some of the cleared land was cultivated, but much remained as pasture. On more fertile soils this led to the development of grassland, but ericaceous species became dominant on the poorer soils. Many heathlands were already formed by the time of the Roman invasion (Rackham, 1986) but expansion continued. There are 21 heaths and a further 26 places named after heaths mentioned in Anglo-Saxon charters (Rackham, 1986). In England, there is evidence of widespread forest clearance around 1100 (Conway, 1957). Heathland as such is not recorded in the Domesday Book, but is incorporated as pasture. For example, Rackham (1986) estimates that 28% of Dorset was pasture, of which one quarter was in the south-east of the county and presumed to be heathland.

In Medieval times, most heathland areas were legally protected as common land. The newly-introduced rabbit ensured the perpetuation of some heaths (Rackham, 1986). Landowners could release rabbits on to commons for commercial profit without violating the rights of the Commoners. For example, Lakenheath Warren in Suffolk was set up in the twelfth century by the Bishop of Ely, Lord of Lakenheath (Crompton and Sheail, 1975).

There was extensive forest clearance in the sixteenth and seventeenth centuries due to the demand for charcoal for iron-ore smelting and timber for ship-building (Gimingham, 1972; Rackham, 1986). By the end of the seventeenth century primary woodland had been severely depleted and heathland had become established on the soils which were unsuitable for cultivation.

1.4. The Historic Use of Heathland

Prior to the agricultural advances of the late seventeenth century onwards, heathland soils were too infertile to cultivate and therefore open heath was used for other purposes. Heathland provided fuel, thatch, rough grazing and animal bedding for many rural communities, who settled and cultivated the more fertile soils within the heathland areas (Webb, 1986).

1.4.1. Fuel-gathering

Until the construction of the railways in the 19th century, fuel had to be obtained from local sources. Heathlands supplied fuel in the form of gorse, heather, bracken and turf (Rackham, 1986; Webb, 1986). Gorse ('furze') in particular was valued for heating ovens. Gorse, heather and bracken were also used as low-grade thatch (Rackham, 1986; Webb, 1986). Bracken provided animal bedding (Tubbs, 1968; Haskins, 1978) and it was burnt for potash on a large scale in the 18th and 19th centuries. The ashes were used in glassmaking, soapmaking, and as a detergent (Rymer, 1976).

Turf and peat cutting (Turbary) were widespread on the Lizard Peninsula in Cornwall (Hopkins, 1983), Dorset (Traynor, 1995) and the New Forest (Tubbs, 1968; 1986). The removal of the upper soil horizons during this process ensured the maintenance of low nutrient levels in the system. Turves were probably cut in the summer and left on the heath to dry for a couple of months (Traynor, 1995). Then the turves were transported by horse and cart to dwellings, and stacked close to one of the external walls (Legg, 1987; Traynor, 1995).

1.4.2. Grazing

Grazing was widespread on the lowland heaths of southern Britain until the middle of the nineteenth century (Webb, 1986). The type of animals that were grazed depended on the locality. Sheep were grazed on the Suffolk Sandlings, Cannock Chase and Breckland in Norfolk. Cattle and sheep were grazed on the Dorset heaths, but superior grazing was available nearby on the chalk downlands. Cattle were most common on the Lizard Peninsula . Ashdown Forest and the New Forest still have ancient Commoners' rights of grazing ponies, pigs and cattle.

Grazing prevented scrub and tree invasion, but probably encouraged the growth of grasses (Webb, 1986). Low nutrient levels in heathland soils were maintained because manure and carcasses were usually deposited elsewhere. The practices of cutting gorse for fodder and rotational burning were associated with grazing, both of which helped to maintain the open nature of heathland.

1.4.3. Burning

The use of fire to manage the heathlands of Scotland and northern England has been established since about 1800 (Gimingham, 1972). Hardy Cheviot sheep became the main domestic herbivore in Scotland around this time and, due to the selective grazing behaviour of sheep, it gradually became necessary to manage heather to maintain its productivity. Grouse-shooting became popular in the mid-19th century when the grouse population began to rise in response to the increase in heathland area. Burning in small patches on a 10 - 15 year rotation was found to provide optimal forage and cover for these game-birds (Gimingham, 1972).

Burning may not have been so common on the southern heaths. There are only occasional records of heath fires (e.g. White, 1789) and legislation existed to prevent them (Rackham, 1986). The traditional uses of heathland such as fuel gathering and grazing may have prevented scrub invasion without the need for burning (Webb, 1986).

Indeed, closely grazed heather would be difficult to burn and the ungrazed areas were required for fuel (Rackham, 1986). Regular burning may have been introduced as late as the 19th century, following the example set in the uplands, possibly in response to the decline in grazing and other activities (Webb, 1986).

1.5. The Decline of Heathland

The agricultural improvements of the late 17th century enabled cultivation of some of the heathland. Open commons and wastelands were enclosed and the use of fertilisers, crop rotations and weed control increased dramatically. Enclosed heathland was often stripped of vegetation, ploughed and burnt. Where heathlands escaped ploughing, the decline in grazing and fuel gathering permitted the invasion of trees and scrub. By the mid-19th century nearly one sixth of Surrey had changed from heathland to woodland (Rackham, 1986). The extent of the Dorset heathlands changed little between Roman times and the mid 18th century (Haskins, 1978), when the area of heath started to decline due to agriculture and afforestation (Moore, 1962; Webb and Haskins, 1980). The expansion of Poole and Bournemouth in the late 19th century covered extensive areas of heathland. The heathlands of the Poole Basin shrank from 40, 000 ha in the mid-18th century to only 5832 ha in 1978 (Webb and Haskins, 1980).

1.6. Methods of management

Today, many of the southern heathland areas are in reserves owned or managed by bodies such as the Royal Society for the Protection of Birds, the Wildlife Trusts and English Nature. The objectives of managing heathland for conservation vary, but the main aim is to obtain a diversity of habitats representing a series of successional stages. In general, scrub invasion is prevented, although stands of mature gorse (*Ulex europaeus*) provide habitat for the rare Dartford Warbler (*Sylvia undata*) (Catchpole and Phillips, 1992). If birch and bracken are invading, control is by cutting and / or herbicide application (Lowday, Marrs and Nevison, 1983; Marrs, 1984; Marrs, 1987; Lowday and Marrs, 1992). The management of heather involves maintenance of low nutrient levels and the creation of a mosaic of growth phases. Management practices today utilise some of the traditional methods of maintaining lowland heath.

1.6.1. Controlled Burning

Burning is often preferred to cutting because it removes some of the litter layer and hence more nutrients, as well as providing a more suitable substrate for seedling establishment (e.g. Mallik, *et al.*, 1988; Mallik, Hobbs and Legg, 1988). It can also be used on any type of terrain and does not require expensive equipment. Regeneration from rootstocks tends to be rapid, providing that the heather is not in the degenerate phase (Kayll and Gimingham, 1965; Hobbs and Gimingham, 1984b; Mohamed and Gimingham, 1970).

The main aim of burning is to create a mosaic of habitats, therefore burning is carried out in strips or scattered blocks of about 10 m in width with sinuous margins. Fire breaks around the areas to be burnt are prepared in advance of burning. These can be permanent features, created by back-burning or rotovating a strip either side of the area to be burnt. Semi-permanent fire-breaks are maintained by regular mowing of the vegetation to a few centimetres in height. This method has the advantage of providing a suitable habitat for many invertebrates such as the silver- studded blue butterfly (*Plebejus argus*). Brush-cutting or forage-harvesting a strip either side of the area to be burnt creates a temporary firebreak and provides material to be added as extra fuel.

Heather burning in England is restricted to the period between 1 November and 31 March. The legal period in Scotland and some upland areas in England extends between 1 October and 15 April. This limits adverse effects on the flora and fauna by avoiding the period of active plant growth and the breeding seasons of reptiles and birds.

Weather conditions determine when burning takes place. Damp vegetation is difficult to ignite and sufficient material may not be removed by burning. However, the vegetation should not be too dry as the risk of the fire getting out of control and igniting the humic layer is increased. Management burning is usually performed in the spring after some frosts have drawn water from the soil. If it has rained or snowed, a few days of fine weather with a drying wind are required before burning. The weather conditions on the day of burning should be dry with no more than a light breeze, preferably fairly constant in speed and direction.

Management burning on southern heaths is usually against the wind (backburning). This tends to produce a hot, slow-moving fire that consumes more of the litter than if burnt with the wind. However, on the moister heaths further north, burning with the wind is usual practice (Gimingham, 1992).

Management fires are started along one edge of the area to be burnt by igniting close-set points with a blow-torch or paraffin burner (Gimingham, 1992). The fire is controlled by personnel with fire beaters (Plate 1.1). If the terrain is suitable, the presence of a tractor-drawn water tank with pump and hoses is an extra precaution (Plate 1.2). Sometimes the surrounding vegetation is sprayed with 'heavy' water (sodium alginate mixed with water), a liquid which is slow to evaporate and so acts as a fire-retardent.

1.6.2. Cutting

Cutting has been advocated as an alternative management method to burning because it is considered less detrimental to vertebrate populations and can be performed at any time of year. The biomass and density of resprouting from rootstocks is similar to regeneration after burning (Gardner, Liepert and Rees, 1993; Cotton and Hale, 1994) but the remaining litter layer may cause nutrient enrichment and hinder seedling establishment. A further disadvantage is that cutting machinery such as double-chop forage harvesters can only be used on fairly even, non-stony ground. The cut material is usually removed to limit nutrient accumulation. This can prove costly, but if cutting is carried out in the autumn, the cut material is a rich seed source which can be used to restore other degraded or disturbed areas (Gimingham, 1992). Cut material can also be used in roof-thatching, bio-filtration, mulches and for footpath renovation in the Pennines (P. Putwain, pers. comm.).

Plate 1.1. Burning at Aylesbeare

Plate 1.2. Burning at Arne with water - bowser on stand-by

1.6.3. Grazing

Sheep grazing is still part of the economy of the Scottish heaths, but grazing has been largely discontinued on the southern lowland heaths. Burning is used in association with grazing, because sheep prefer young, more nutritious heather to older plants (Grant and Hunter, 1968). Grant and Armstrong (1993), working on sheep grazing in Scotland, found that up to 40% of the current season's shoots of young heather could be eaten with no effect on the productivity of heather the following season. Recently, there has been considerable interest in introducing stock to lowland heath. In Dorset, heathland areas managed by English Nature are now grazed by cattle and ponies (Graham, Alexander and Nicholson, 1997). Grazing opens up the vegetation, prevents scrub invasion, encourages low-growing plants and promotes growth of ericaceous species (Bullock and Pakeman, 1997). However, under- or over-grazing can be damaging to heather and the choice of animal should be carefully considered (Gimingham, 1992).

1.6.4. Turf-cutting

Turf-cutting has the advantage of removing nutrients and creating areas of bare ground which are important for some invertebrates and reptiles. The surface of the mineral soil, especially on the sheltered edges of the turf pit, provides a less hostile environment for seedling establishment than an exposed litter surface (Traynor, 1995). Turf-cutting creates small-scale heterogeneity in vegetation structure and reliance on seedling establishment enhances genetic diversity. Traditionally, turves were removed with a sharp-edged spade, but now machines such as long-arm excavators can remove large areas. The cut turves can be used in restoration of damaged heathland or to create new areas of heath (Michael, 1993).

1.6.5 Rotovation

Rotovation has been used to regenerate old heather in Cannock Chase and Breckland (Michael, 1993) but is not frequently used elsewhere except as a method of creating permanent fire breaks. This method does not remove nutrients from the system and regeneration depends on seedling establishment.

1.7. The Effects of Severe Fires

The impacts of accidental summer fires and the controlled burning carried out in the autumn and spring are very different. Accidental fires are predictably more common on the heaths closest to habitation (Farrell, 1993) and are most severe after a period of drought. A wild fire can cross firebreaks and roads, so large areas can be burnt in one fire; for example, 60 ha of Arne Heath, Dorset, in 1973 (B. Pickess, pers. comm.) and the nearby Hartland Moor in 1976. Hot fires that burn large areas are lethal to most of the heathland fauna that have no means of escape (Muirburn Working Party, 1977; Hobbs and Gimingham, 1987) and can cause local extinctions.

The risk of severe fire tends to increase with the age of the vegetation. A stand with a high proportion of dry woody material is very flammable and burns at high temperatures (Kenworthy, 1963). Such severe fires can ignite the humic layer, causing excessive loss of nutrients and destroying the rootstocks and seed bank of the ericaceous species (Radley, 1965; Maltby, 1980; Clement and Touffet, 1981). Hence subsequent regeneration depends on the aerial input of seed. The development of a bryophyte cover has been observed after severe fires in 1976 in Brittany (Clement and Touffet, 1981, 1990; Gloaguen, 1990, 1993) and in North Yorkshire (Maltby, 1980, Maltby, Legg and Proctor, 1990). The mosses may inhibit colonisation by other species and persist for some time (e.g. 13 years, Gloaguen, 1993). In upland areas, erosion can be extensive (Kinako and Gimingham, 1980; Maltby, 1980; Maltby *et al.* 1990). However, even severe fires are heterogeneous and less severely-burnt areas can recover more rapidly. On a landscape scale, areas of Dorset heathland burnt in 1976 had returned to their pre-burn composition by 1987 (Bullock and Webb, 1995).

1.8. Rationale for this work

The decline in burning on the southern lowland heaths is due to several factors, including fears of detrimental effects on reptile populations (N. Webb, pers. comm.), encouraging birch and bracken invasion (Rackham, 1986) and diminishing visual amenity (Harrison, 1976). In areas close to the urban fringe, the area that is 'accidentally' burnt every year may be more than would require management (P. Edgar, pers. comm.). Auld, Davies and Pickess (1992) state that burning is inadvisable on all but the largest heathland sites. There are less likely to be local extinctions on larger sites, because there is more surrounding heathland from which re-colonisation can occur. Cutting is often used instead of burning (P. Edgar, N. Gartshore, C. Marrable, R. McGibbon, pers. comms.) but burning is more economical, removes more nutrients in the vegetation and litter and can be performed on uneven terrain (Gimingham, 1992).

Moore (1962) states that "probably the most important effect of the decline of rough grazing has been the virtual extinction of controlled burning which used to accompany it". The area of heathland in Dorset that is burnt each year has declined further since Moore's 1960 survey. Between May 1959 and May 1960, approximately 8% of the heathland existing at that time was burnt (Moore, 1962). The 1978 survey described by Webb and Haskins (1980) found only 13.6% of the existing heathland had been burnt in the preceding two years. It was estimated that 11% of this was in 1976, when there were extensive accidental fires. In the two years preceding the heathland survey of 1987 (Webb, 1990), only 6% of the area had been burnt. The 15% increase in scrub that occurred between the 1978 and 1987 surveys was partly attributed to the decline in burning (Webb, 1990).

The main aim of this study was to elucidate the effects of fire temperature and stand age on vegetation dynamics following management burning. Vegetation fuel loads were manipulated at mature and degenerate stands of vegetation in Dorset and Devon to test the hypothesis that fire temperatures and intensity depend chiefly on fuel load rather than other factors associated with the pre-burn age of the stand.

Chapter Two introduces the study sites in Dorset and Devon, including their geology, vegetation and management history. The experimental burning and resultant fire temperatures and intensity are described in Chapter Three. The results of two burning experiments, using different methods of temperature recording, are presented. A third experiment tests the accuracy of one of the methods.

Chapter Four investigates the effects of burning on soil nutrients and the seed bank contained in the litter and soil. The quantities of calcium, magnesium and phosphorus present in the ash and humus immediately after burning are presented. The seed bank remaining in the litter and soil after burning represents the main source of propagules for seedling regeneration following burning.

Vegetative regeneration following burning is described in Chapter Five. Biomass, cover, growth and flowering are considered in relation to the growth phase of the burnt vegetation and to fire temperature.

The demography of the ericaceous seedlings that germinated after burning is explored in Chapter Six. The effects of fire temperature and vegetative regeneration on seedling establishment and survival is investigated. Microclimatic data of bare ground compared with the shelter of resprouting vegetation are presented and are used to describe the conditions experienced by emerging seedlings. Chapter Seven is a general discussion and the applicability of burning as a management technique is considered.

CHAPTER TWO

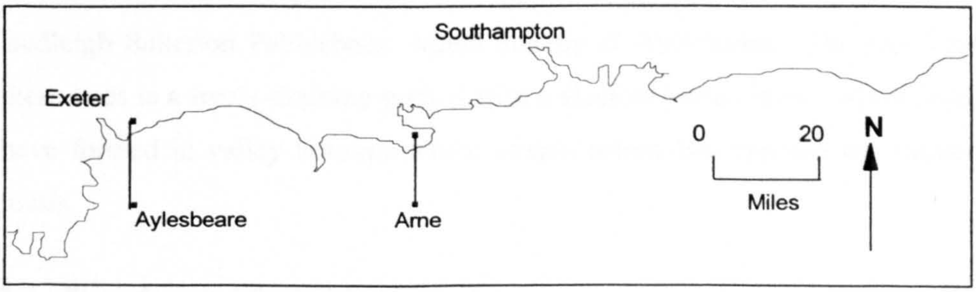
Study Sites

2.1. Introduction

The experimental sites were two geographically separate areas of dry lowland heath in southern England: Arne in Dorset (grid reference SY973882) and Aylesbeare Common in Devon (grid reference SY059903). Figure 2.1 shows the location of the two study sites. Arne has been managed by the RSPB since 1966 and contains approximately 340 ha of heathland. The reserve occupies a peninsula which extends into Poole Harbour and encompasses areas of woodland and salt marsh. There is a plantation of Scot's Pine (*Pinus sylvestris*) next to the western edge of Arne Heath. The southern edge of Coombe Heath is contiguous with Hartland Moor National Nature Reserve.

Ratcliffe (1977) describes Aylesbeare Common as the "best example of a series of heathlands known as the East Devon or Pebble Bed Commons". The 184 ha of Aylesbeare and Harpford Commons are owned by Clinton Devon Estates and have been managed together by the RSPB since 1977. The reserve includes areas of wet and dry heath with associated mires and basic flushes. There is also woodland at the edge of the reserve.

Fig. 2.1. Map of southern England, show location of Arne and Aylesbeare



2.2. Geology and Soils

2.2.1. Arne

The heaths of south-east Dorset, Hampshire and Surrey occur on the Tertiary deposits of the Hampshire Basin. These deposits consist mainly of sand, clay, loam, limestone bands, shell bands and pebbles. The London Clays and Reading Beds form the edges of the Basin and are made up of sands and clay. Here the soils are fertile brown earths and surface-water gleys. Overlying these beds are the Bracklesham and Bagshot Beds. The Bracklesham Beds are exposed in Hampshire but in south-east Dorset only the yellow and white sands of the older Bagshot Beds are exposed. Freely-draining humus-iron podsols, characteristic of dry heathland, have formed on these beds. Clay lenses covering areas up to several hectares and 5 - 15 m thick occur within the Bagshot Beds. Where the clay is close to the ground surface, drainage is impeded gleyed soils have developed. In valley areas this may encourage the development of peat and the growth of humid or wet heathland.

2.2.2. Aylesbeare

The geology of south-east Devon is dominated by Permian (286 - 245 Ma) and Triassic (245 - 208 Ma) deposits. The Permian deposits of sandstones, marls, conglomerates and breccias outcrop in the west of the area and are overlain by Triassic marls and sandstones to the east. These Triassic deposits are made up of Bunter Beds and Keuper Marls and Sandstones. The Bunter Beds include the Budleigh Salterton Pebblebeds, which outcrop at Aylesbeare. The soil formed on these beds is a freely-draining podsol with a shallow humic layer. More fertile soils have formed in valley bottoms where stream action has exposed the impermeable marls.

2.3. Experimental Design

Stands of mature and degenerate heath were selected at both reserves (Figs 2.2 and 2.3, Plates 2.1 - 2.4). The degenerate stands had been unmanaged for at least 50 years. The mature stand at Arne was burnt accidentally in 1973 and was comparable in structure to the mature stand at Aylesbeare, last burnt in 1981. The stands were fairly homogeneous in vegetation structure and composition, but any obvious differences between plots were noted.

Fig. 2.2 Map of Arne, showing location of mature and degenerate stands (adapted from Traynor, 1995)

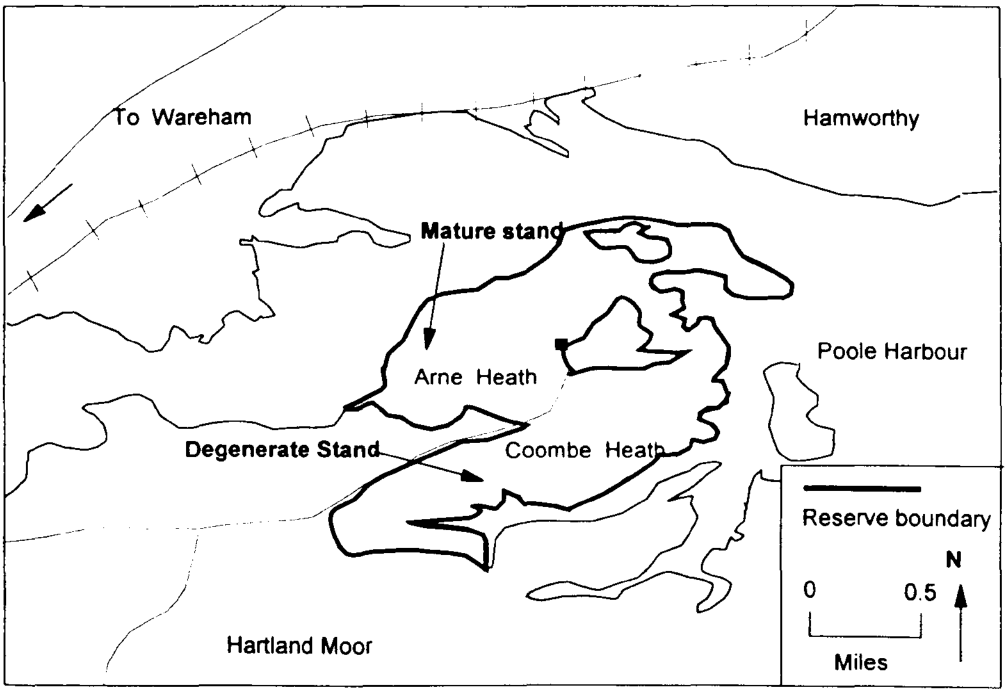
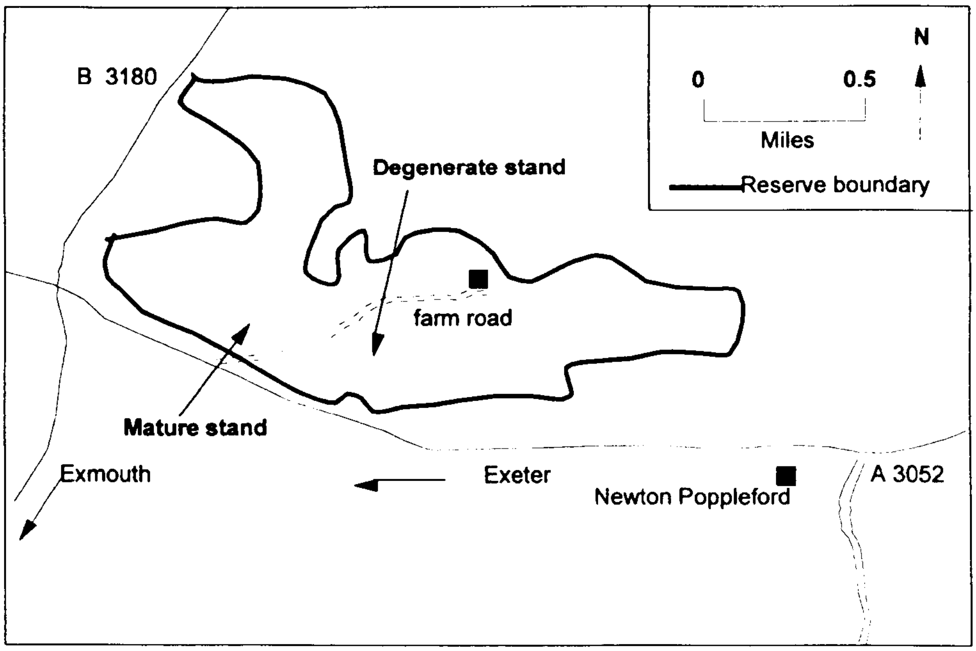


Fig. 2.3. Map of Aylesbeare, showing location of mature and degenerate stands (adapted from Traynor,1995)



Controlled burning at both Arne and Aylesbeare is usually carried out in strips of about 10 metres wide surrounded by narrower forage-harvested or brush-cut strips which behave as fire breaks. Therefore the experimental design at each stand incorporated the experimental plots into a single strip where space allowed (Figs 2.4 and 2.5). Twelve plots of 5 x 5 m were marked out at each stand in November 1993 ready for burning in spring 1994. The plots were separated by 3m to minimise ash drift during burning. A randomised block design was employed, with two fuel load treatments (low and high) plus a control in each of four blocks. The plots for the spring 1995 fires were marked out in January 1995 in a strip adjacent to the 1994 plots at the mature stand at Aylesbeare. These plots were 3m x 2m in four blocks of three plots. There were two burning treatments of 0.75 l of paraffin per plot and no added paraffin, plus an unburnt control in each block.

Plate 2.1. The mature stand at Arne

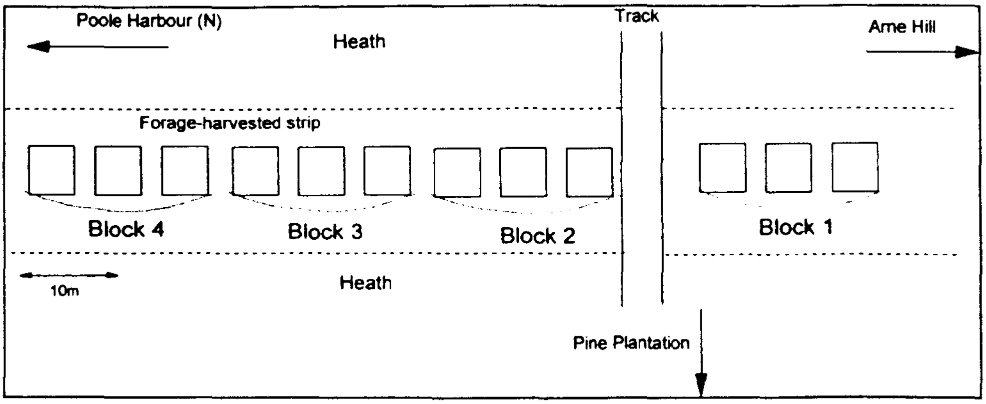
Plate 2.2. The degenerate stand at Arne

Plate 2.3. The mature stand at Aylesbeare

Plate 2.4. The degenerate stand at Aylesbeare

Fig. 2.4. Plot layout at Arne

Mature Stand



Degenerate Stand

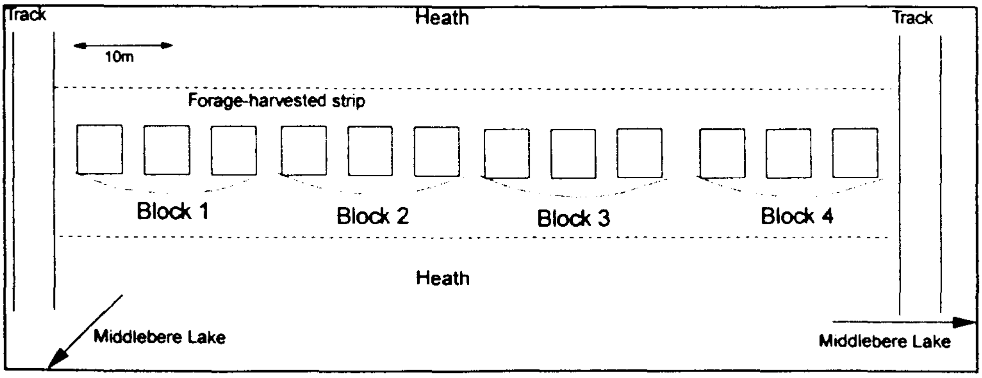
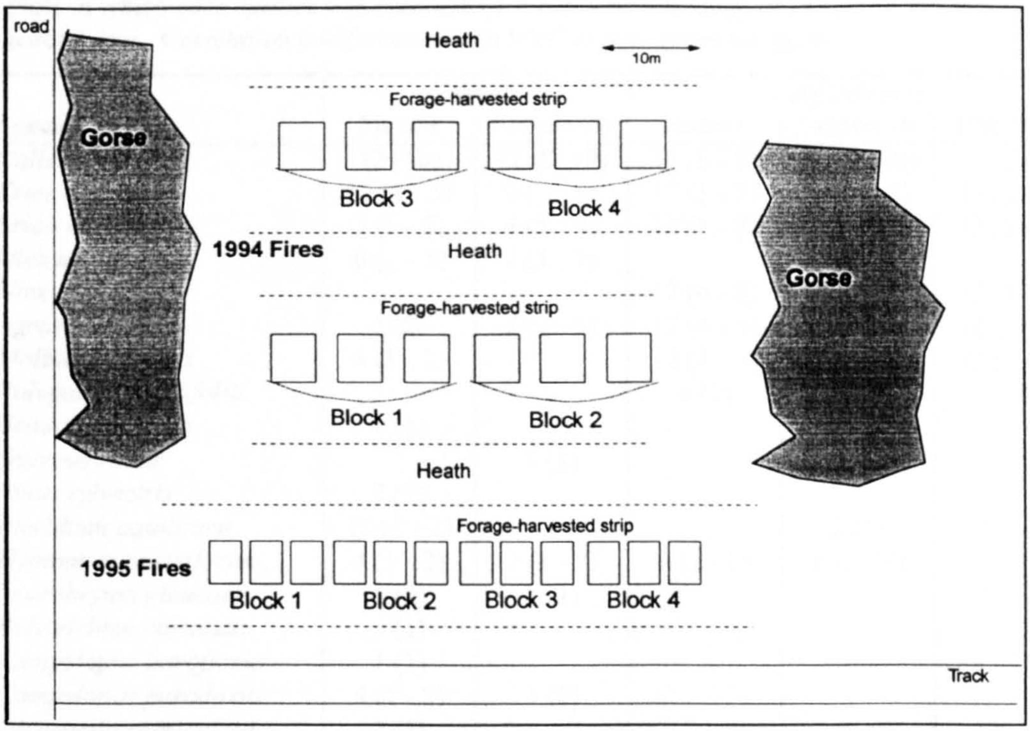
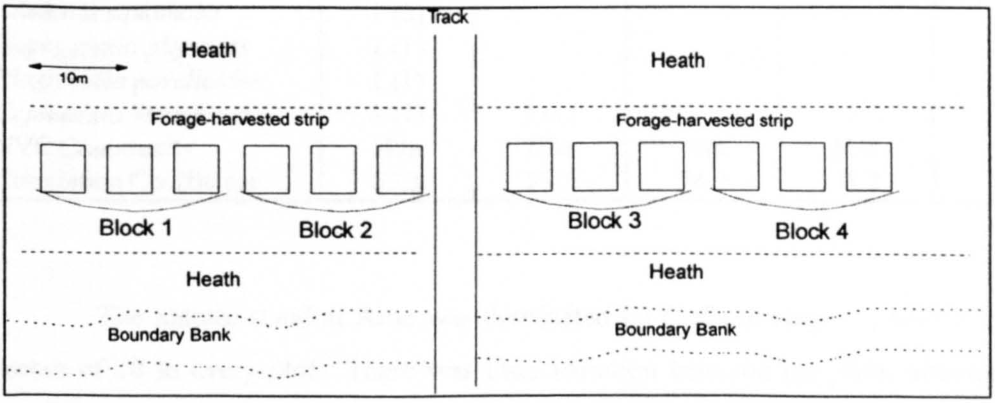


Fig. 2.5. Plot layout at Aylesbeare

Mature Stand



Degenerate Stand



2.4 Vegetation Survey

The vegetation of the stands was surveyed using each 5 x 5m plot (1994 fires) or 3 x 2m plot (1995 fires) as a quadrat and assigning Domin scores to each species. The twelve 'quadrats' from each stand were compared with the National Vegetation Classification (NVC), (Rodwell, 1991) using 'Match' (Malloch, 1992). Species composition at each stand and the correlation with NVC communities are shown in Table 2.1.

Table 2.1. Frequency and cover of species at the study sites. Figures are the number of plots in which each species was recorded (n = 12), with the range of Domin scores in parentheses. Correlation coeffiecients with NVC communities are given.

	Arne		**Aylesbeare**		
Species	**Mature**	**Degenerate**	**Mature**	**Degenerate**	**1995 Fires**
Calluna vulgaris	12 (10)	12 (8 -10)	12 (5 - 7)	12 (5 - 10)	12 (5 - 7)
Erica cinerea	12 (1 - 3)	9 (2 - 4)	12 (1 - 5)	12 (5 - 6)	11 (2 - 4)
Erica tetralix	3 (1 - 3)	4 (1 - 4)	12 (1 - 8)	1 (1)	12 (5 - 8)
Ulex minor	8 (1 - 3)	7 (1 - 3)			
Ulex gallii			12 (4 - 8)	12 (5 - 7)	12 (5 - 7)
Agrostis curtisii	1 (2)	4 (1 - 3)	12 (4 - 5)	12 (1 - 5)	12 (2 - 7)
Molinia caerulea	4 (1 - 2)		12 (1 - 5)	11 (1 - 7)	12 (1 - 5)
Polygala serpyllifolia			4 (1)		2 (1)
Betula pubescens	1 (1)				
Quercus robur		1 (1)			
Pinus sylvestris	7 (1)				
Pteridium aquilinum	12 (1 - 2)			2 (1)	
Hypnum cupressiforme	4 (1 - 2)	7 (1 - 2)	3 (1 - 2)	4 (1 - 2)	
Leucobryum glaucum	1 (2)	1 (1)			
Polytrichum commune	1 (1)				
Campylopus introflexus	1 (1)				
Campylopus paradoxus	4 (1 - 2)	1 (2)			
Dicranella cerviculata	2 (2)				
Dicranum scoparium	3 (1 - 2)	3 (2 - 3)			
Cladonia impexa	12 (2 - 3)	8 (1 - 2)	2 (1)		5 (1 - 2)
Cladonia pyxidata / fimbriata	9 (2 - 3)	7 (1 - 2)			
Cladonia squamosa	1 (2)				
Hypogymnia physodes	1 (1)				
Plagiochila porelloides	1 (1)				
Cephalozia bicuspidata	1 (1)	1 (1)			
NVC Community	H2a	H2a	H4c	H4a	H4c
Correlation Coefficient	53.3	54.1	74.9	78.2	75.5

The mature stand at Arne was dominated by *Calluna vulgaris*, with a Domin score of 10 in every plot. There was little variation between the plots, although the vegetation in the three plots closest to Poole Harbour (block four) was taller than in the other plots. The vegetation height in block 4 was 0.6 - 0.8m high, compared with 0.3 - 0.5 m high in the other plots. The vegetation composition correlated with H2a *Calluna vulgaris/ Ulex minor* heath, typical sub-community (correlation coefficient 53.3). There was a ground layer of *Cladonia* spp. and mosses including *Campylopus paradoxus* and *Hypnum cupressiforme*. This stand is close to the boundary with a neighbouring plantation and *Pinus sylvestris* saplings were found in over half of the plots. Bracken (*Pteridium aquilinum)* is scattered throughout the area, and occurs in all the plots. The litter layer was fairly even and consisted of quite fine material of about 1 cm depth.

At the Arne degenerate stand many of the heather bushes had died back from the centre, creating an heterogeneous structure with some bare ground (approximately 25% in each plot). *Erica cinerea* accompanied *Calluna* as a constant species. *Ulex minor* was also frequent. At one end of the strip (block 4). *E. tetralix* was present, indicating damper conditions. *Cladonia* spp. were frequent and the bryophyte flora was dominated by *Hypnum cupressiforme*. The litter layer was about 4 cm in depth. 'Match' generated a correlation coefficient of 54.1 with to H2a *Calluna vulgaris / Ulex minor* heath (typical sub-community).

There were fewer species of bryophyte and lichen at Aylesbeare compared with Arne. The layering of heather at Aylesbeare may have prevented the growth of some lower plants through competition as well as obscuring the ground layer in places. The mature stand at Aylesbeare was very homogeneous in structure, with a closed canopy of about 80 cm in height. *Calluna, Erica tetralix* and *Ulex gallii* were co-dominant. *Agrostis curtisii, Molinia caerulea* were constant and occured at high cover in all plots. *Erica cinerea* was constant but at variable cover. Layering of the vegetation was evident; whereby shoots were growing from horizontal stems. The litter layer was only about 1 cm deep. Comparison with the NVC revealed a high correlation with H4c *Ulex gallii/ Agrostis curtisii* heath, *Erica tetralix* sub-community (correlation coefficient = 74.9).

The plots burnt in the 1995 fires were also surveyed, producing a correlation coefficient of 75.5 with the same sub-community. However, *Molinia caerulea* was constant in these plots (Table 2.1), possibly indicating damper conditions than in the neighbouring plots burnt in 1994.

Calluna, Erica cinerea and *Ulex gallii* were co-dominant at the Aylesbeare degenerate stand. The grasses *Agrostis curtisii* and *Molinia caerulea* were constant but at low cover in all plots except block 4, where *Molinia* occurred at 10 - 25% cover.

There is no record of burning this site, so the gorse and heather bushes had grown to nearly a metre in height with thick stems spreading horizontally within the deep (4 - 6cm) an uneven litter layer. The centres of some of the heather bushes had died, but not to the extent of the degenerate stand at Arne. There was a high correlation with H4a *Ulex gallii* / *Agrostis curtisii* heath, *Agrostis curtisii* /*Erica cinerea* sub-community (correlation coefficient = 78.2).

2.5. Vegetation and Litter Biomass

The 1994 experiment involved manipulation of the vegetation fuel load to create two treatments of high and low fuel. Therefore it was essential to know the vegetation biomass at each stand. Quadrats of 0.5 x 0.5m were harvested from immediately adjacent to each plot. The samples were sorted into species and oven-dried to constant weight at 60°C. The litter biomass was estimated by taking 5 samples from each plot with a corer of 11cm diameter and drying to constant weight at 60°C.

The biomass of both the vegetation and litter was greater at the degenerate stands than at the mature stands and a higher percentage of vegetation consisted of woody material (Table 2.2). The biomass of the individual species reflects the Domin scores assigned during the vegetation survey. The data for total vegetation biomass were used in the calculation of the amount of fuel to be added or removed before burning (Chapter Three).

Table 2.2. Vegetation biomass before manipulation. Values are means ± 1 SE in gm^{-2} dry weight (n=12).

	Arne		**Aylesbeare**	
Species	**Mature**	**Degenerate**	**Mature**	**Degenerate**
Calluna vulgaris	1244± 63.4	1653 ± 79.4	435 ± 63.0	611 ± 152
Erica cinerea	17.7 ± 8.3	99.2 ± 38.1	20.9 ± 8.1	1199 ± 141
Erica tetralix	0.0 ± 0.0	17.8 ± 11.9	370 ± 27.8	0.0 ± 0.0
Ulex minor	7.2 ± 5.6	17.1 ± 17.1	0.0 ± 0.0	0.0 ± 0.0
Ulex gallii	0.0 ± 0.0	0.0 ± 0.0	336 ± 54.3	373 ± 80.0
Agrostis curtisii	0.0 ± 0.0	1.1 ±1.1	54.7 ± 12.3	20.9 ± 13.8
Molinia caerulea	3.3 ± 3.3	0.0 ± 0.0	28.0 ± 9.0	11.7 ± 10.3
Pteridium aquilinum	2.5 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Polygala serpyllifolia	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Cladonia sp.	2.9 ± 1.5	1.9 ± 1.6	0.0 ± 0.0	0.0 ± 0.0
Total Vegetation	1278 ± 61.6	1791 ± 108	1245 ± 78.5	2215 ± 152
Percentage woody	20.7 ± 1.5	24.5± 2.5	16.10 ± 1.5	21.7 ± 2.7
Litter	1049 ± 64.5	2410 ± 133	715 ± 51.7	2078 ± 125

CHAPTER THREE

The effects of fuel load and growth phase on fire temperature and intensity

3.1 Introduction

Controlled burning of lowland heathlands has been traditionally used to promote regrowth of nutritious young shoots for domestic stock (Farrell, 1993). Grazing was ubiquitous across the southern lowland heaths in the 18th century (Webb, 1986). The decline of grazing since the 19th century (Moore, 1962) has been matched by a decrease in burning. Controlled burning, where it does occur, is used to arrest succession to scrub and to create structural diversity by breaking up even-aged stands (Gimingham, 1992). It also helps to retain the nutrient-poor status of the heathland system by removing most of the above-ground biomass (Allen, 1964). Heather burning (muirburn) is still common at higher altitudes on moorland in the north of England and Scotland where the aim is provide forage for sheep and red grouse *(Lagopus lagopus scoticus).* Heathland fires in the Scottish uplands have been well studied (e.g. Whittaker, 1961; Kenworthy, 1963; Kayll and Gimingham 1965; Kayll, 1966; Mallik and Gimingham 1983; Hobbs and Gimingham 1984a, Hobbs, Currall and Gimingham, 1984). In contrast, there has been no work on the characteristics of management fires on southern lowland heaths.

Fire temperature is likely to influence post-fire regeneration both from rootstocks and from seed, so it is of interest to know temperatures reached in management fires and means of achieving such temperatures. Fires that are too cool may not burn sufficient vegetation and old stems, which may hinder seedling germination and vegetative regeneration (Muirburn Working Party, 1977). Fires hotter than 300°C may remove litter and humus, causing death of the rootstock and seeds as well as loss of nitrogen and other nutrients in smoke (Kenworthy, 1963; Evans and Allen, 1971).

The duration of elevated temperatures affects the amount of heat which penetrates the soil (DeBano, Dunn and Conrad, 1977). Hobbs & Gimingham

(1984a) measured the durations of temperatures above 400°C in heath fires of only 30 seconds - 1 minute. The litter and soil are subjected to elevated temperatures for longer than the canopy although the maximum temperature reached declines rapidly with depth (Bradstock and Auld, 1995, Raison *et al.* 1986). The former may be because the litter layer often continues to smoulder (glowing combustion) following flaming combustion (van Wagner, 1972; Johnson and Miyanishi, 1995).

Temperature has been frequently used as an indication of the 'intensity' of fires (Sparling and Smith 1966; Stinson & Wright, 1969; Smith and James 1978; Cole, Klick and Pavlovic, 1992; Ramsay and Oxley, 1996). However, temperature is only one aspect of fire behaviour and provides no information on heat flux (Alexander, 1982) or the overall energy output (Whelan, 1995).

Fire intensity was first defined by Byram (1959) as the rate of energy (or heat) release per unit time per unit length of fire front. It is determined by the heat of combustion (energy content, Jg^{-1}) of the fuel and the rate of heat energy release (Trollope, 1984). The energy released per unit weight of fuel is less than the heat of combustion due to unburnt material remaining in ash and lost in smoke as well as the energy required to remove fuel moisture (Alexander, 1982). The rate of energy release is determined by the rate of spread of the fire i.e. the rate at which flames move into the fuel (Johnson and Miyanishi, 1995).

The heat released per unit area is another way of expressing intensity and refers to the heat directed to the surface litter and the fire effects in the litter and soil (Rothermel and Deeming, 1980). It is defined as the amount of heat released by burning a unit area of a given fuel bed (Albini, 1976) and is equivalent to the product of the fuel load consumed and the heat yield of the fuel.

Some studies (e.g. Cheney, 1981; Armour, Bunting and Neuenschwander, 1984; Moreno and Oechel, 1991; Bidwell and Engle, 1992; Glitzenstein *et al.* 1995; Marsden-Smedley and Catchpole, 1995) have employed the concept of fire intensity and its relation to fuel characteristics and weather conditions. These studies are on prescribed burning for fuel reduction or large wildfires in Australian and American forests. Only Kayll (1966) and Hobbs and Gimingham (1984a) have used the concept in heathland fires in the British Isles. However, the measure of energy output as fire intensity may obscure ecologically-important variation in peak temperature and duration (Whelan, 1995), so both fire temperatures and intensity are useful expressions of fire behaviour.

Temperatures of controlled heathland fires have been recorded using thermocouples (Kenworthy, 1963; Kayll, 1966), or pellets, paints and crayons which change colour or melt at specified temperatures (Whittaker, 1961; Hobbs, Currall and Gimingham, 1984). Thermocouples have the advantage of a high degree of accuracy and can record the duration of temperatures, but are expensive. 'Pyrometers' of temperature-sensitive materials painted on substrates such as aluminium, mica or ceramic tiles are an inexpensive way to estimate temperature but their accuracy is limited to the temperature interval between the paints selected and the response times of the paints (Hobbs & Gimingham 1984a).

Fuel load is thought to be the most important variable governing fire temperature and intensity (Kayll, 1966; Sparling and Smith, 1966; Grant, 1968; Fonteyn *et al.*, 1984, Hobbs and Gimingham, 1984a; Hobbs, Currall and Gimingham, 1984; Moreno and Oechel, 1991). In heathlands, vegetation biomass and heterogeneity are generally greater in degenerate than in building or mature phase heath (Hobbs and Gimingham, 1984a). Thick stems constitute a high proportion of the biomass in old degenerate heath and bushes begin to die off fom the middle, creating gaps in the vegetation. Hobbs and Gimingham (1984a) stress that fuel distribution, as well as biomass, is important in determining fire behaviour. Studies on Scottish heathlands (e.g. Kenworthy, 1963; Hobbs and Gimingham, 1984a and b) did not replicate fires within stands or standardise fuel load and vegetation composition. Furthermore these experiments were performed on different days under different weather conditions.

In this study, replicated plots within homogeneous stands were burnt on the same day. By replicating within stands, there is the disadvantage of having to burn small plots, but the factors affecting fire intensity such as fuel, weather, topography and fire history (Whelan, 1995) are similar between treatments. These variables are determined ultimately by the amount of energy stored as living and dead biomass per unit area (Whelan, 1995). Therefore, in this investigation, vegetation fuel load was hypothesised to be the main factor controlling fire behaviour. This was tested in the first experiment by manipulating vegetation biomass in mature and degenerate stands of heath to provide high and low fuel load treatments. Temperatures were measured in this experiment with pyrometers consisting of temperature-sensitive paints and crayons on tiles. The second experiment used the novel approach of adding paraffin as a substitute fuel load and aimed to compare the recording capabilities of pyrometers with thermocouples. A third experiment tested the sensitivity of the pyrometers by examining the range of temperature - time combinations at which the paints and crayons would melt. The temperatures indicated by the pyrometers may have been under-estimates if the paints did not melt instantly on exposure to their specified temperatures. These data were used to interpret the fire temperature pyrometer data under different exposure time scenarios.

3.2. Methods

3.2.1. Experiment 1. 1994 Fires

Mature and degenerate stands of vegetation were selected at two sites: Arne in Dorset and Aylesbeare in Devon (Chapter Two). Twelve plots of 5 x 5 m were laid out in a strip at each stand separated from one another by 3m to minimise ash drift. Vegetation was forage harvested in 3m widths either side of the strips to act as fire breaks. Vegetation biomass was estimated at all sites by harvesting one quadrat of 0.5 x 0.5m from immediately adjacent to each plot (Chapter Two). The samples were sorted into species and oven-dried to constant weight at 60°C. The litter biomass was estimated by taking 5 samples from each plot with a corer of 11cm diameter and drying to constant weight at 60°C.

The 12 plots in each stand were divided into four blocks and three treatments were applied according to a randomised block design. The treatments were an unburnt control and two burning treatments using high and low fuel loads. The control plots were used in post-fire monitoring of seedling demography, but are not referred to further in this chapter. Fuel loads were altered by adding or removing vegetation. The vegetation biomass data (Table 2.2 in Chapter Two) were used to calculate these fuel loads. At both Arne and Aylesbeare the biomass was greater at the degenerate stands than at the younger stands. The high fuel load treatment was designated as the existing biomass of the degenerate stand at each site. The low fuel load treatment was made equivalent to the existing biomass at the mature stands. Vegetation biomass was manipulated to achieve these treatments. The fuel load treatments are summarised in Table 3.1.

Table 3.1. Summary of the fuel load treatments

	Treatment	
Stand	**Low Fuel Load**	**High Fuel Load**
Mature	Burn existing vegetation	Add vegetation
Degenerate	Remove vegetation	Burn existing vegetation

Table 3.2 shows the estimations of fuel load to be added to the high fuel load treatment at the mature stands and to be removed from the low fuel load treatment at the degenerate stands. The high fuel load treatment on the mature stands was achieved by adding vegetation brush-cut from an known area (Table 3.2) adjacent to each plot. The added material was trodden down into the vegetation so that it did not alter the overall vegetation height. The relevant proportion of bushes were removed from the low fuel load treatment plots on the degenerate stands by cutting bushes at ground level. Care was taken to remove the bushes in an even pattern.

Table 3.2 Estimation of fuel load addition and removal. Values of vegetation and litter biomass are means in gm^{-2} (from Table 2.2, Chapter Two)

	Arne	**Aylesbeare**
Vegetation biomass at mature stand /g m^{-2}	1278.2	1245.2
Vegetation biomass at degenerate stand /g m^{-2}	1791.0	2215.0
Difference in biomass / g m^{-2}	512.8	969.8
Mature Stands		
% Biomass to be added to high fuel load plots	40.12	77.88
Area to be added to high fuel load plots /m^{2}	10.02	19.50
Degenerate Stands		
% of bushes to be removed from low fuel load plots	28.63	43.78

Pyrometers were constructed using paints (Tempilaq°) and crayons (Tempilstiks°)* of specific melting points in strips on 20 x 20cm floor tiles (Plate 3.1). Tempilstiks° are cheaper and easier to use, but may evaporate or be absorbed under prolonged heating or at temperatures above 371°C. The paints (Tempilaq°) were therefore favoured, although a few low temperature crayons were used due to paints being out of stock. The following were painted onto the tiles: 38°C, 52°C (crayons), 62°C, 87°C (paints), 101°C (crayon), 135°C (paint), 204°C (crayon), 246°C, 302°C, 343°C, 500°C, 621°C, 704°C and 1038°C (paints). These paints were chosen to encompass the range of temperatures expected in controlled burning (e.g. Whittaker, 1961; Hobbs, Currall and Gimingham 1984).

Three pyrometers were positioned randomly in each treatment plot immediately before fires were started. They were inserted in the ground to a depth of 6 cm so that a temperature profile up to a maximum of 14 cm above ground could be determined. The methods used to light and extinguish the fires depended on the equipment available at the two sites. Fires were lit with matches and extinguished with beaters at Aylesbeare but a flame gun and a water bowser were available at Arne. Each fire was burnt against the wind (back-burnt). The tiles were removed when cool and the positions of the soil and litter surfaces marked. Then the minimum height at which each paint / crayon strip had melted was recorded. Continuous measurements of wind speed and direction were made during burning using an anemometer. Ambient temperature and relative humidity were recorded immediately before burning at each stand. One sample each of vegetation, litter and soil was taken for analysis of moisture contents from each plot just before the plots were burnt. The vegetation samples were taken from near the top of the-canopy and included both woody and green material. Litter and soil samples were taken with a trowel. The fresh weight of these samples was determined, and then the samples were dried at 105°C for 48 hours and % weight loss calculated.

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* Manufacturers: Tempil° Division, Big Three Industries Inc., 2901 Hamilton Blvd., South Plainfield, New Jersey 07080 USA. British Distributor: Optimum Heat Control Ltd., Mere House, Mere Park, Dedmere Road, Marlow, Bucks. SL7 1PD.

Plate 3.1. Pyrometer with strips of temperature - sensitive paints after burning

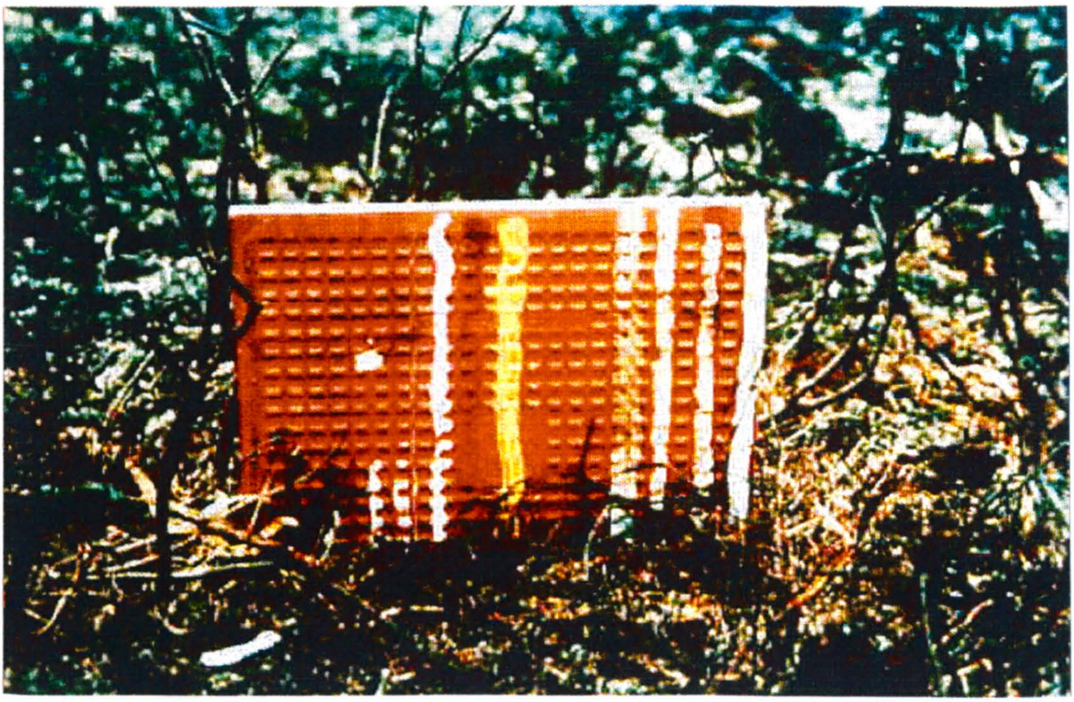
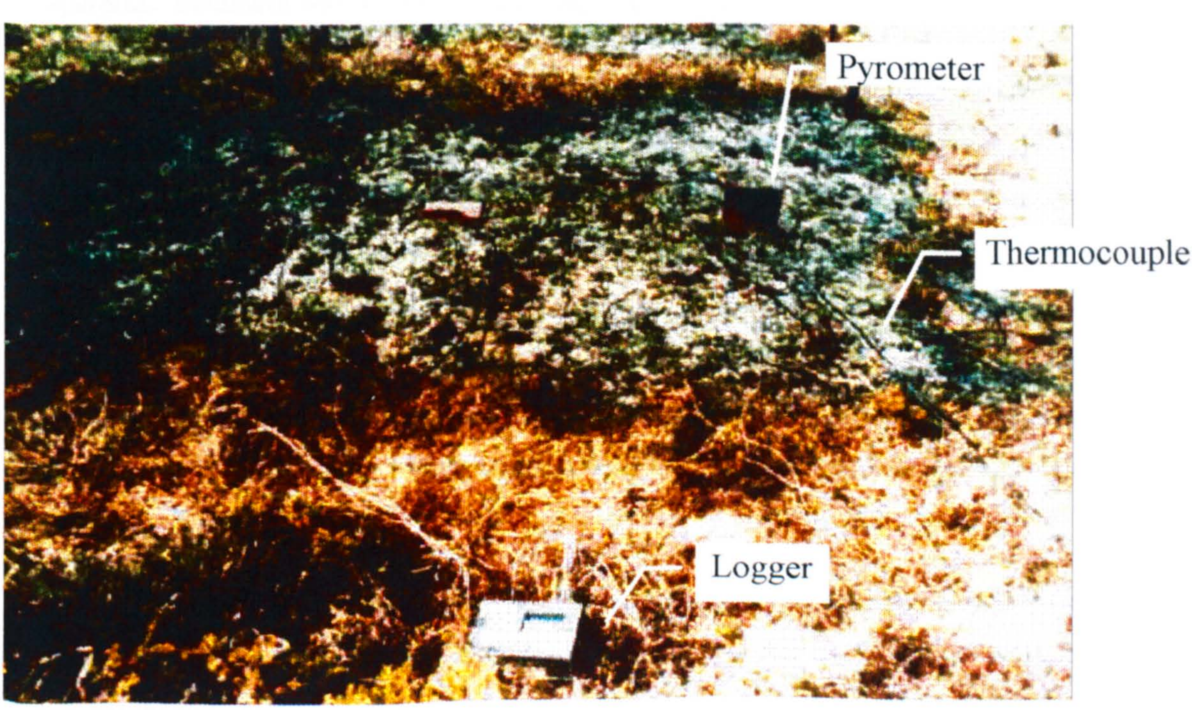


Plate 3.2. Logger, thermocouples and tiles after burning at Aylesbeare in 1995



The fuel load remaining after burning was estimated by harvesting unburnt stems from two randomly-positioned quadrats of 0.1 x 1m in each plot. Long narrow quadrats were selected to encompass heterogeneity of the burnt plots. Samples of unburnt stems were taken in 1994, 1995 and 1996 and separated from the vegetative regrowth that was also harvested (Chapter Five). The litter biomass left after burning was assessed by taking 5 samples from each plot with the same corer as was used before burning. Stem and litter samples were dried to constant weight at 60°C and the biomass per m^2 calculated. There were no significant differences between the three years of stem samples, so means were taken to provide a better estimate.

3.2.2. Experiment 2: 1995 Fires

Only the Aylesbeare Mature stand was used for the second experiment in March 1995. A strip of twelve plots of 3m x 2m was set up adjacent to the plots burnt in 1994. A randomised block design of two burnt treatments plus unburnt controls was employed. Using a knapsack sprayer, 0.75 l (0.125 l m^{-2}) of paraffin was evenly distributed across each of the four '+ paraffin' treatment plots. The '-paraffin' treatment was to burn the existing vegetation.

Before lighting each fire eight base-metal thermocouples were positioned in the plot, four just beneath the litter surface and four immediately above them, resting in the canopy. The thermocouples were 2m in length (so that the cables were not exposed to fire) and were connected to a Squirrel Data Logger (1200 Model, Grant Instruments, Cambridge) (Plate 3.2). Each pair of thermocouples was placed in approximately the same position in each fire, about 1m apart from one another in the centre of each plot. Three pyrometers were placed alongside three pairs of thermocouples in each plot. Fires were lit with a blow torch and extinguished with beaters.

The available fuel load was not measured directly, because the biomass was assumed to be similar to the adjacent plots. The unburnt fuel load was estimated by harvesting two randomly-positioned quadrats of 0.1 x 1m from each plot and drying to constant weight. Samples were taken in 1995 and 1996. There were no significant differences between the two, so means were used as a measure of unburnt fuel.

3.2.3. Experiment 3: Sensitivity of paints and crayons

Temperatures between 60 and 800°C in 30°C increments were tested at exposure times of 1, 2, 3 and 4 minutes in an oven (up to 300°C) and muffle furnace (300 - 800°C). Three pyrometers were tested for each temperature / time combination. Paints were recorded as having melted when all three pyrometers had responded. The pyrometers were allowed to cool to the ambient temperature of about 8°C before being used again. The inevitable drop in temperature as the door of the oven or muffle furnace was opened meant that the precise temperature to which the tiles were exposed was slightly less than the specified temperature. The effect of a drop in temperature becomes more important the shorter the exposure time, which is why one minute was judged to be the shortest time that could be tested with any confidence.

3.2.4. Data Analysis

The vegetation consumed by fire in each plot was estimated by subtracting the biomass of stems remaining after fire from the available fuel load. The biomass of litter consumed (1994 fires only) was calculated for each plot by subracting the mean biomass after burning from the mean biomass before burning.

The moisture contents of litter, soil and vegetation on the day of burning were compared between stands at both sites using one-way ANOVA. Least significant differences (LSD) using Bonferroni's Adjustment were used to test comparisons.

The fire intensity equation of Byram (1959) defines fire intensity as the rate of energy or heat release per unit time per unit length of fire front. The equation is:

$$I = Hwr \qquad (1)$$

where I is the fire intensity (Wm^{-1}), H is the heat of combustion of the fuel (Jg^{-1}), w is the fuel load consumed (gm^{-2}) and r is the rate of forward spread of the fire front (ms^{-1}). Measurement of rate of spread requires that fires have reached a steady-state of flow (Rothermel and Deeming, 1980, Cheney, 1981). Due to the size of the plots in this investigation and the fact that some fires were re-lit if they were going out, it was unlikely that a steady-state was reached. Therefore, the heat released per unit area was used to express intensity:

$$H_A = H_{corr} w \qquad (2)$$

where H_A is the heat released per unit area ($J\ m^{-2}$), *Hcorr* is the heat yield of the fuel, which is equivalent to the heat of combustion corrected for latent heat of vaporisation and moisture content of the fuel (Alexander, 1982), and w is the fuel load consumed (gm^{-2}). The heat of combustion of vegetation does not vary a great deal between species (Trollope 1984), so a value for *Calluna* of 22.4 kJg^{-1} (ITE Merlewood Analytical Chemistry Section) was used as an overall value, rather than calculating heat yields for individual species and fuel types. The corrections made to the heat of combustion were a constant value of 1263 Jg^{-1} for the latent heat of vaporisation and 24 Jg^{-1} per moisture content percentage point (Alexander, 1982).

The moisture contents of the litter, soil and vegetation on the days of burning were compared between stands using one-way ANOVA followed by calculation of least significant differences (LSD) at an experiment-wise error rate of 0.05 using Bonferroni's Adjustment (Maxwell and Delany, 1990). Fuel and intensity variables in the 1994 fires were checked for normality and homogeneity of variances before performing nested analysis of variance (ANOVA). The percentage of vegetation consumed was arcsine transformed. Transforming the two variables biomass of litter consumed and the percentage of litter consumed could not make them fit the assumptions of ANOVA, so these data were analysed using Friedman tests to compare treatments and Mann-Whitney tests to compare stands. Temperature data were also analysed using Friedman and Mann-Whitney tests because of the non-uniform increments between paints. Fire temperatures and total energy released were tested for correlations using Spearman-Rank correlation coefficients.

The effect of paraffin on temperatures in the 1995 fires was analysed using Friedman tests for the pyrometer data and ANOVA for the thermocouple data. The two temperature data sets were compared with a Spearman Rank Correlation. The fuel load remaining after burning was tested for treatment differences using ANOVA.

3.3. Results

3.3.1. Experiment 1: 1994 Fires

Weather conditions and fuel moisture status on days of experiments

Burning was carried out at Arne on March 26th 1994 and at Aylesbeare on March 24th 1994. Rain had fallen at Arne two days prior to this date and at Aylesbeare the previous day. The vegetation and soil moisture contents at the two sites were similar, but the litter moisture content was significantly different between stands (Table 3.3). Calculation of least significant differences using Bonferroni's adjustment revealed that stands within site were similar to one another, but the litter moisture content at Aylesbeare was significantly higher than that at Arne (LSD = 6.89, 28 df, significant at experiment -wise error rate of 0.05).

Table 3.3 Fuel moisture contents (%). Values are means for all plots at each stand (n=12, ± SE). F-value = results of one - way ANOVA comparing the four stands.
** = 0.001 < P < 0.01, NS = not significant.

Site / Stand	**Moisture Contents (% dry weight)**		
	Vegetation	**Litter**	**Soil**
Arne Mature	43.20 ± 1.04	56.17 ± 3.42	62.42 ± 3.47
Arne Degenerate	40.89 ± 1.85	55.67 ± 2.98	52.39 ± 4.35
Aylesbeare Mature	42.01 ± 1.31	71.70 ± 0.44	53.61 ± 4.99
Aylesbeare Degenerate	37.73 ± 1.65	67.87 ± 1.73	45.05 ± 5.28
F-value	2.17 NS	8.75 **	2.12 NS

Weather conditions for each stand are shown in Table 3.4. The order in which the stands were burnt at the two sites was determined by the site managers on the basis of access and manpower. At Arne, the degenerate stand was burnt in the morning and the mature in the afternoon. The order was reversed at Aylesbeare. There was little difference between morning and afternoon at either site in temperature or relative humidity, but the wind dropped slightly at both sites in the afternoon.

Table 3.4 Weather conditions at each stand at time of burning

Site / Stand	Wind speed (ms^{-1})	Ambient temperature (^{o}C)	Relative humidity (%)
Arne Mature (pm)	1.74	15	55
Arne Degenerate (am)	2.31	16	65
Aylesbeare Mature (am)	4.63	11	65
Aylesbeare Degenerate (pm)	3.00	12	65

Fire Temperatures

The temperatures presented here are the means of the highest point at which paints melted at the soil and litter surface and in the portion of the tile above ground. The absolute temperature may be higher than this (up to the next highest melting point paint), so these data are conservative estimates. When no paints had melted (lowest melting point = 38°C), usually because the vegetation around the pyrometer remained unburnt, an arbitrary temperature of $5^{0}C$ has been selected on the basis that this was the approximate ambient temperature of the litter. The means and ranges of temperatures recorded by pyrometers in each plot are shown in Appendix One.

Fire temperatures were higher above ground than at the soil or litter surface at both stands at both sites (Table 3.5). Friedman tests comparing treatments showed that high fuel load fires were usually hotter than low fuel load fires in all stands except the Aylesbeare degenerate stand. At Arne, there were significant differences between the treatments in both stands at the litter surface and above ground. The results of the Mann-Whitney tests in Table 3.6 show that the two fuel load treatments produced similar temperatures at both stands, although soil temperatures in the low fuel load treatment were significantly higher in the mature stand than in the degenerate stand.

Temperatures recorded at all vertical positions in high fuel load fires at the Aylesbeare mature stand were significantly hotter than those in the low fuel load fires (Table 3.5). Litter surface and maximum above ground temperatures were hotter in the high fuel load treatment in the mature stand than in the same treatment in the degenerate stand (Table 3.6). There were no significant differences between stands in the low fuel load treatment. Soil surface temperatures were not compared statistically because none of the paints melted at the degenerate stand, although temperatures at the mature stand seemed to be higher.

Table 3.5. Mean maximum fire temperatures at soil and litter surfaces and above-ground (0-14cm). Values are means ± standard errors with the range of values in parentheses. S = Friedman Statistic comparing fuel load treatments. NS = not significant, * = $0.01 < P < 0.05$

Site / Stand	**Vertical Position**	**Temperature (^{0}C)**		**S**
		Low fuel	**High fuel**	
Arne Mature	Soil Surface	39.8 ± 6.5 (5 - 62)	64.6± 23.6 (5 - 204)	1.00 NS
	Litter Surface	81.0 ± 13.5 (38 - 204)	162.8 ± 70.3 (38 - 704)	4.00 *
	Above-ground	393.0 ± 81.9 (135 - 1038)	581.4 ± 67.0 (204 - 704)	4.00 *
Arne Degenerate	Soil Surface	9.8 ± 4.8 (5 - 62)	36.7 ± 15.4 (5 - 101)	3.00 NS
	Litter Surface	48.3 ± 11.9 (5 - 101)	112.3 ± 23.3 (62 - 246)	4.00 *
	Above-ground	173.9 ± 31.1 (62 - 204)	444.8 ± 8.2 (343 - 704)	4.00 *
Aylesbeare Mature	Soil Surface	15.3 ± 7.1 (5 - 62)	54.3 ± 13.6 (5 - 135)	4.00 *
	Litter Surface	32.75± 9.86 (5 - 87)	88.7 ± 19.8 (38 - 204)	4.00 *
	Above-ground	178.1 ± 8.07 (62 - 343)	396.2 ± 77.9 (149 - 704)	4.00 *
Aylesbeare Degenerate	Soil Surface	5.0 ± 0.0 no paints melted	5.0 ± 0.0 no paints melted	0.00 NS
	Litter Surface	19.17 ± 6.22 (5 - 62)	21.93 ± 5.93 (5 - 62)	0.33 NS
	Above-ground	207.9 ± 57.6 (62 - 704)	154.75 ± 7.39 (101 - 204)	0.00 NS

The fires at Aylesbeare were in some cases cooler than those at the corresponding stands at Arne (Table 3.5). The litter surface and maximum temperatures in the low fuel load treatment at the Arne mature stand were significantly higher than in the same treatment at the Aylesbeare mature stand (Table 3.6). However, there were no significant differences between the high fuel load fires. Comparing the degenerate stands revealed that the high fuel load treatment at Arne was significantly hotter than Aylesbeare at the litter surface and above ground (Mann-

Whitney test: P = 0.03), but there was no difference between the low fuel load treatments.

Table 3.6. Mann-Whitney W statistics comparing stands and sites. LF = Low fuel load fires, HF = High fuel load fires. Comparisons with soil surface temperatures at the Aylesbeare degenerate stand could not be made, because no paints melted at the soil surface at this stand.

Comparison		**Vertical position**		
		Soil surface	Litter surface	Above-ground
Arne Mature v.	LF	24.5 NS	26.0 *	26.0 *
Aylesbeare Mature	HF	17.0 NS	20.0 NS	23.0 NS
Arne Degnerate v.	LF	-	24.5 NS	17.0 NS
Aylesbeare Degenerate	HF	-	26.0 *	26.0 *
Arne Mature v.	LF	25.5 *	22.0 NS	25.0 NS
Arne Degenerate	HF	20.0 NS	18.5 NS	22.0 NS
Aylesbeare Mature v.	LF	-	22.0 NS	18.0 NS
Aylesbeare Degenerate	HF	-	26.0 *	26.0 *

Fire behaviour and intensity

Table 3.7 shows the fuel loads available and consumed by the fires, as well as the estimated heat released per unit area.

Table 3.7. Fire behaviour characteristics. Section A = mean values (n=4) ± SE. Section B = Nested ANOVAs. Mean square of stand (block) used as denominator to calculate F-value of stand.

A. Site/ stand	**Fuel load**	**Vegetation fuel load available (gm^{-2})**	**Litter fuel load (gm^{-2})**	**Vegetation fuel load consumed (gm^{-2})**	**% Vegetation fuel load consumed**	**Litter fuel load consumed (gm^{-2})**	**% Litter fuel load consumed**	**Heat released per unit area (vegetation only, kJm^{-2})**
Arne Mature	Low	1222 ± 167	1177 ± 167	1134 ± 161	92.58 ± 1.39	48.0 ± 218	8.40 ± 16.70	22637 ± 3237
	High	2265 ± 141	1023 ± 49.2	2200 ± 137	97.16 ± 0.83	97.3 ± 81.1	9.61 ± 7.72	43681 ± 2738
Arne Degenerate	Low	1096 ± 127	2117 ± 166	1031 ±125	94.32 ± 3.94	-7.0 ± 118	-	20580 ± 2476
	High	1783 ± 194	2659 ± 275	1724 ±212	96.18 ± 1.73	538 ± 194	19.43 ±5.35	34386 ± 4245
Aylesbeare Mature	Low	1307 ± 81.8	692 ± 33.2	1171 ± 68.1	89.65 ± 1.21	120 ± 45.2	18.17 ± 6.95	23577 ± 1175
	High	2625 ± 119	752 ± 73.2	2516 ± 114	95.85 ± 0.47	41.2 ±58.5	4.52 ± 8.95	50176 ± 2276
Aylesbeare Degenerate	Low	1200 ± 229	1946 ± 29.2	891 ± 198	72.03 ± 5.81	355 ±257	17.90 ± 12.80	17857 ± 3975
	High	2125 ± 69.7	2208 ± 165	1864 ± 38.9	88.01 ± 3.25	624 ± 185	27.40 ± 6.58	37343 ± 794
B. ANOVA	**df**							
Arne								
Stand	1	3.78 NS	46.75 **	3.53 NS	0.54 NS	See text	See text	3.35 NS
Fuel load	1	28.59 **	1.06 NS	26.86 **	1.09 NS			26.55 **
Block (stand)	6	0.94 NS	0.88 NS	0.83 NS	0.42 NS			0.84 NS
Stand x fuel load	1	1.21 NS	3.42 NS	1.21 NS	0.50 NS			1.14 NS
Aylesbeare								
Stand	1	3.67 NS	162.51 **	15.87 **	103.17 **			16.29 **
Fuel load	1	90.38 **	4.32 NS	86.57 **	7.14 *			85.43 **
Block (stand)	6	1.81 NS	1.89 NS	0.88 NS	0.08 NS			0.85 NS
Stand x fuel load	1	2.77 NS	1.70 NS	2.22 NS	0.53 NS			2.04 NS

The available fuel load was significantly different between treatments at both stands at Arne and Aylesbeare (Table 3.7). There was no significant difference between stands at either site, so manipulating vegetation biomass was successful in generating both high and low fuel load treatments that were similar in available fuel at both stands. Litter fuel load available only differed significantly between stands. This was to be expected, since no manipulation of litter was performed.

A linear regression between the fuel load consumed and the fuel load available was significant ($r^2=0.756$, $n = 32$, $p < 0.001$), so the fuel load burnt during the fires is also significantly different between treatments at both stands at both sites. Fuel load consumed was significantly different between stands at Aylesbeare, but not at Arne.

At Arne, the proportion of the available fuel consumed did not differ significantly between treatments. At Aylesbeare, however, there was a difference between stands and an overall difference between treatments at both stands (Table 3.7).

The biomass of litter consumed was extremely variable, and subtracting the mean litter biomass per plot after burning ($n =5$) from the mean biomass per plot before burning produced negative values, indicating that no litter had been consumed in some plots. The data for litter biomass consumed and percentage litter biomass consumed were not normally distributed and variances were not homogenous, even under transformation. Non-parametric Mann-Whitney tests were employed to compare stands at the two sites and Friedman tests to compare treatments within each stand (Table 3.8). There was no significant difference between the two stands at Arne in either the amount or the percentage of litter fuel load consumed. At Aylesbeare, the fuel load removed was significantly larger in the degenerate stand than in the mature stand (Table 3.7 and 3.8) but there was no difference in the proportions. There were no differences between low and high fuel load fires in either variable at either of the mature stands (Table 3.8). Both the amount and the percentage of litter biomass burnt off was greater in high fuel load fires than in low fuel load fires at the Arne degenerate stand. However, at the Aylesbeare degenerate stand, the percentage removed was not significantly different between treatments. Since the amount of litter consumed by fire relative to the pre-burn biomass was so small and variable (Table 3.7), litter consumption was not used to estimate energy release by the fires.

Table 3.8. Stand and treatment comparisons of litter fuel load consumed and percentage litter fuel load consumed. Section A = Mann-Whitney 'W' statistic to compare stands. Section B = Friedman 'S' statistic to compare treatments within stands

Comparison	Variable Litter Fuel Load Consumed	 % Litter Fuel Load Consumed
A. Stands (Mann-Whitney)		
Arne	59.0 NS	69.0 NS
Aylesbeare	47.0 *	60.0 NS
B. Treatments (Friedman)		
Arne Mature	0.00 NS	0.00 NS
Arne Degenerate	4.00 *	4.00 *
Aylesbeare Mature	0.00 NS	1.00 NS
Aylesbeare Degenerate	4.00 *	1.00 NS

Vegetation moisture values used to calculate the heat yield (H_{corr}) of the vegetation are in Table 3.3. As the heat yield only varies with moisture content, and this was not affected by the treatments, the main source of variation in heat released is the vegetation fuel load consumed (linear regression: $r^2 = 99.98\%$, $P < 0.001$). Therefore the ANOVA for heat released per unit area revealed similar patterns to the ANOVA for fuel load consumed. The fuel load treatment had a significant effect at both stands (Table 3.7). At Aylesbeare, there was a significant difference between stands as well as between treatments, but there was no stand x treatment interaction.

The total heat released per unit area by the low fuel load treatment fires was around 20 MJm^{-2} at all the stands except the Aylesbeare degenerate stand (Table 3.7). Here fires were noticeably less intense, at around 18 MJm^{-2}. The high fuel load treatment at the Aylesbeare mature stand produced the most heat energy. Although this treatment had a similar fuel load to the same treatment at the degenerate stand, a greater proportion of the available fuel load was consumed, generating 13 MJm^{-2} more than the high fuel load fires at the degenerate stand.

Due to departures from normality and homoscedacity, it was not possible to perform linear regressions on fire temperatures and other fire behaviour variables. Instead, Spearman rank correlation coefficients were computed for temperatures recorded by the pyrometers and the variables percentage of available fuel load consumed, fuel load consumed and heat released per unit area (which are themselves highly correlated). Table 3.9 demonstrates the positive correlations between temperatures recorded at different heights in the profile and fire intensity variables. There were no significant correlations between fire temperatures and fuel moisture contents.

Table 3.9. Spearman Rank Correlation Coefficients and their significance (n =32, df =30). ** = 0.001 < P < 0.01, * = 0.01 < P < 0.05.

	Temperature Variable		
'Intensity' Variable	**Soil**	**Litter**	**Maximum above-ground**
% Available Fuel Load consumed	0.506 **	0.628 **	0.462 **
Vegetation Consumed	0.550 **	0.414 *	0.493 **
Heat Released per Unit Area	0.540 **	0.398 *	0.482 **

3.3.2. Experiment 2: 1995 Fires

Table 3.10. Temperatures in Aylesbeare 1995 Fires. Values are means ±SE. Pyrometer data tested with Friedman test (S) and thermocouple data with ANOVA (F). n=4, all 1 d.f.

	Pyrometer			**Thermocouple**		
Position	**Low Fuel Load Fires**	**High Fuel Load Fires**	**S**	**Low Fuel Load Fires**	**High Fuel Load Fires**	**F**
Soil Surface	23.9 ± 4.0 (5 - 62)	80.6 ± 29.7 (5 - 246)	4.00*	15.24 ± 8.48 (2.62 - 40.20)	16.38 ± 5.63 (7.13 - 31.50)	0.01 NS
Litter Surface	295.0 ± 140 (5 - 704)	220.0 ± 127.0 (38 - 1038)	1.00 NS	-	-	-
Above-ground	433.9 ± 89.3 (101 - 343)	469.0 ±129.0 (101 - 1038)	1.00 NS	632.8 ± 43.0 (511.0 - 698.4)	604.1 ± 34.5 (514.0 - 668.0)	0.24 NS

Adding 0.75 l of paraffin made no significant difference to fire temperatures recorded by either the pyrometers or thermocouples at any of the vertical positions, except the soil surface recording made by the pyrometers (Table 3.10 The temperatures recorded by the pyrometers were very different to those recorded by the thermocouples. The thermocouples inserted in the litter recorded lower temperatures

than those indicated by the pyrometers at either the litter or soil surface. Conversely, the above-ground temperatures recorded by the thermocouples were around 200°C higher than those of the pyrometers.

There were no significant differences between treatments for either duration of temperatures above 400°C or the total duration of fires. However, paraffin did seem to encourage faster burning. Plots with paraffin added burnt for a mean of 10.25 min (± 3.66 SE), compared with 15.75 min. (± 2.17 SE) when no paraffin was added. Two of the paraffin-added fires took only 4 minutes to burn the whole plot. The mean duration of temperatures above 400°C was around 1.5 min for both treatments (87.5 s ± 11.1 for non paraffin fires and 97.5 s ± 10.7 for added paraffin fires).

The mean biomass remaining was very similar whether or not paraffin was added ($P = 0.910$). Therefore fuel consumed and hence heat released per unit area were also not affected. Using the mean of the adjacent strip of plots which were burnt the previous year (1245 gm^{-2}) as an estimate of available fuel load the mean vegetation consumed was 1148 gm^{-2} (92.2%) in fires without paraffin and 1141 gm^{-2} (91.7%) in fires with added paraffin.

3.3.3. Experiment 3: Paint sensitivity

Figure 3.1 illustrates that none of the Tempilaq° paints and Tempilstiks° melted at their specified temperatures even at exposure times of 4 minutes. The 621°C paint did not melt at 800°C under a 1 min exposure. The 704°C did not melt at this temperature at 1 or 2 minutes exposure. The 1038°C paint was not tested.

For most paints / crayons, there was little difference in melting point between 2 and 4 minutes exposure. The percentage difference between actual and specified melting points at these exposure times varied (Fig. 3.2), but was about 50% for paints of specified melting points less than 300°C and 20 - 30% for paints of higher melting points. The percentage differences for the 1 minute exposure were generally very high (100 - 200%) for paints / crayons of melting points 149°C and less. Paints with specified melting points of 204 - 343°C melted at about double their specified

Fig. 3.1. Melting points of Tempilaq° paints and Tempilstiks° at different exposure times.
? = paint did not melt

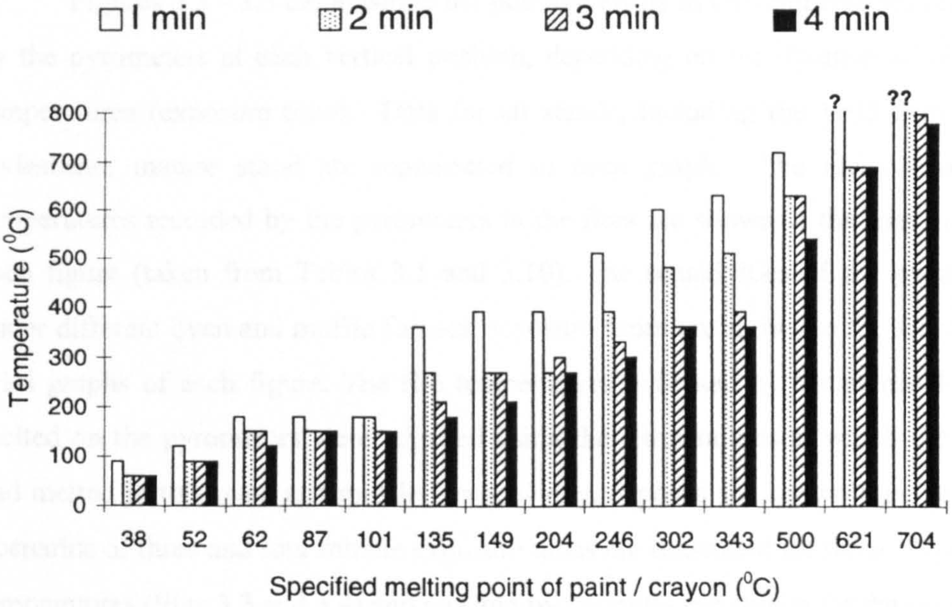
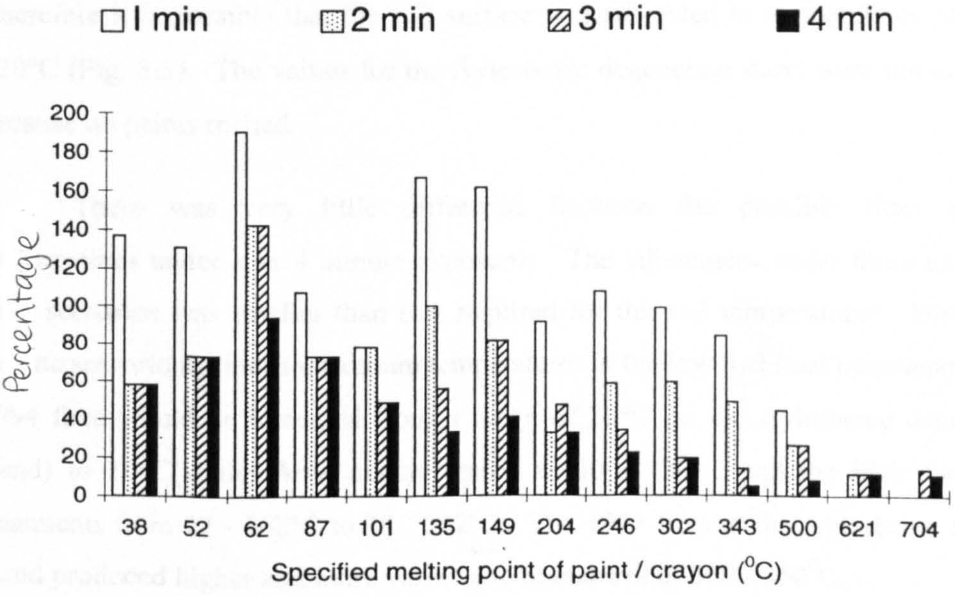


Fig.3.2. Percentage difference between actual and specified melting points of Tempilaq° paints and Tempilstiks°



melting points under a 1 minute exposure. The 500°C paint was the highest melting - point paint to melt at all at this exposure time and had an error of around 50%.

Figures 3.3 - 3.5 demonstrate the possible errors in the temperatures recorded by the pyrometers at each vertical position, depending on the duration of elevated temperatures (exposure time). Data for all stands, including the 1995 fires at the Aylesbeare mature stand are represented in each graph. The mean maximum temperatures recorded by the pyrometers in the fires are shown in the first graph of each figure (taken from Tables 3.5 and 3.10). The sensitivities of the pyrometers under different oven and muffle furnace exposure times are shown in the second and third graphs of each figure. The fire temperatures indicated by the paints that had melted on the pyrometers were adjusted using the temperatures at which the paints had melted in this oven and muffle furnace when exposed for known time periods. Scenarios of three and four minute exposure times are illustrated for the soil and litter temperatures (Figs 3.3 and 3.4) and one and two minutes are shown for the maximum above-ground temperatures (Fig. 3.5). These exposure times were selected based on data in the literature and the duration of elevated temperatures measured in the 1995 fires.

Soil temperatures recorded by pyrometers would be doubled under a 3 min exposure and were increased by just less than 50% under a 4 min exposure. Therefore it is possible that the soil surface was subjected to temperatures of up to 120°C (Fig. 3.3). The values for the Aylesbeare degenerate stand were not adjusted because no paints melted.

There was very little difference between the possible litter surface temperatures under 3 or 4 minute exposures. The adjustment under these exposure time scenarios was smaller than that required for the soil temperatures. Under a 3 minute scenario the mean maximum temperatures in the low fuel load treatments in the 1994 fires would be increased from a range of 20°C (at the Aylesbeare degenerate stand) to 80°C(at the Arne mature stand) to 30 - 130°C and the high fuel load treatments from 22 - 162°C to 38 - 242°C. The 1995 fires at the Aylesbeare mature stand produced higher and more variable temperatures of 300 - 350^{0}C.

Fig. 3.3. Soil temperatures recorded by pyrometers and suggested adjustments under exposure times of 3 and 4 minutes. Values are means ± 1 SE. ArM = Arne mature stand, ArD = Arne degenerate stand, AyM = Aylesbeare mature stand, AyD = Aylesbeare degenerate stand, AyM95 = 1995 fires at the Aylesbeare mature stand.

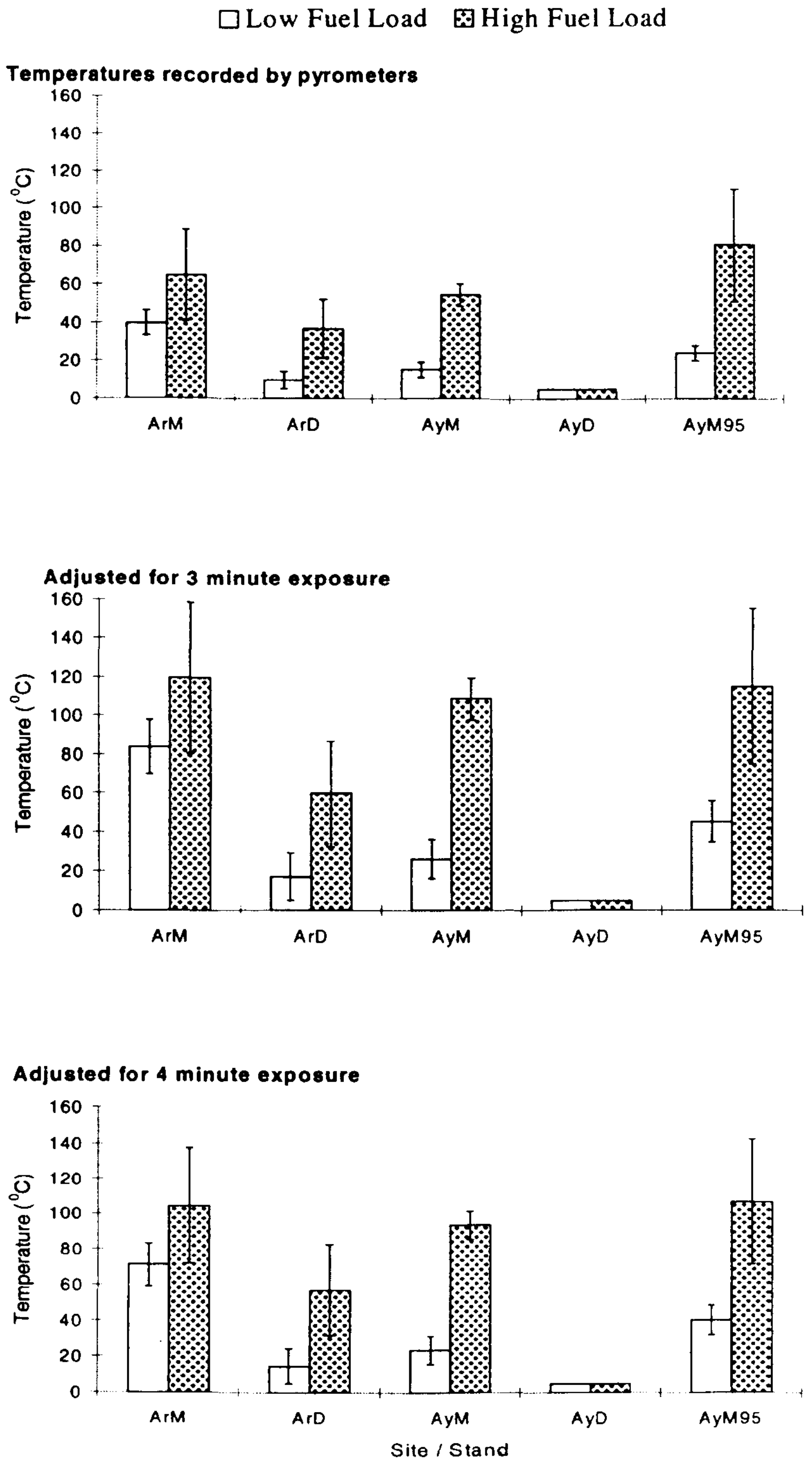


Fig. 3.4. Litter temperatures recorded by pyrometers and suggested adjustments under exposure times of 3 and 4 minutes. For legend see Fig. 3.3.

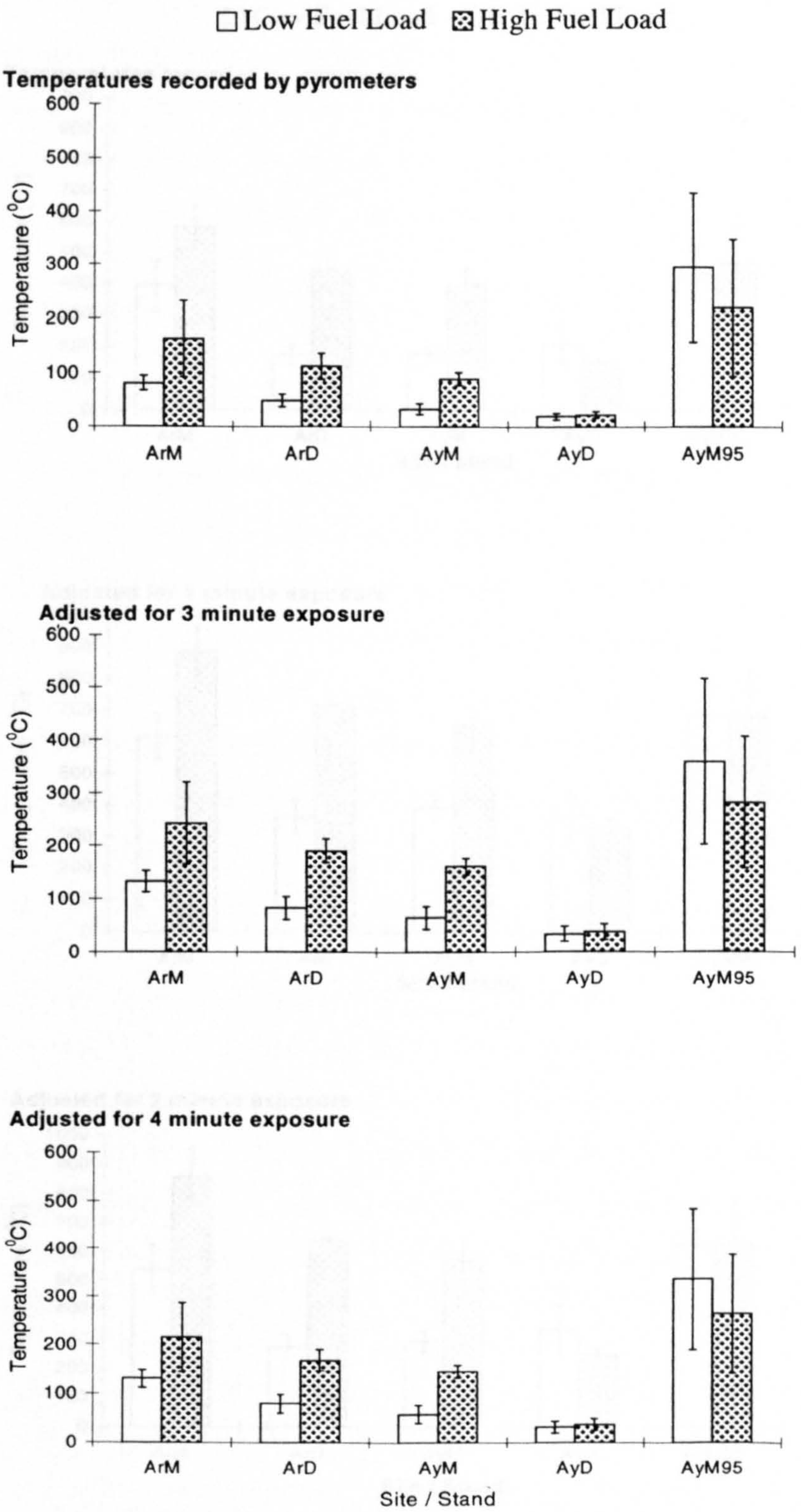
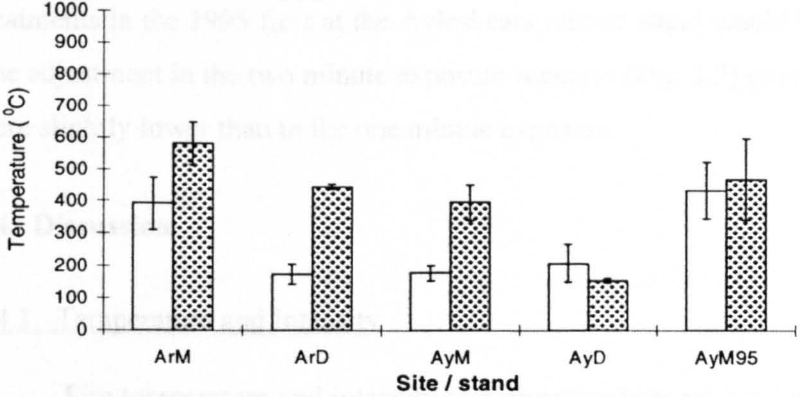


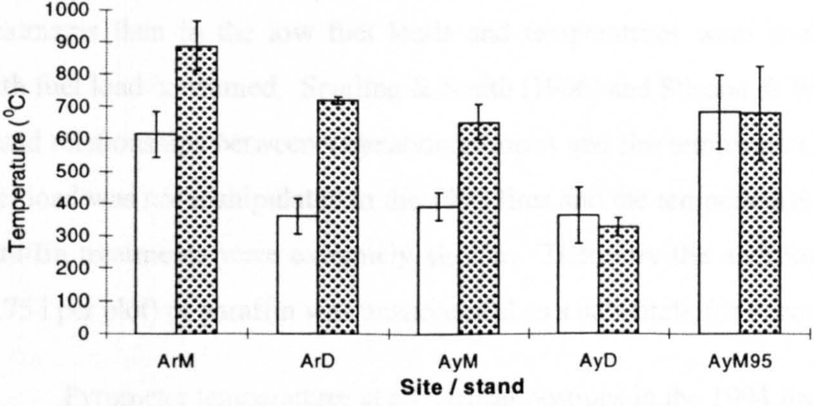
Fig. 3.5. Maximum above-ground temperatures recorded by pyrometers and suggested adjustments under exposure times of 1 and 2 minutes. For legend see Fig. 3.3.

□ Low Fuel Load ▨ High Fuel Load

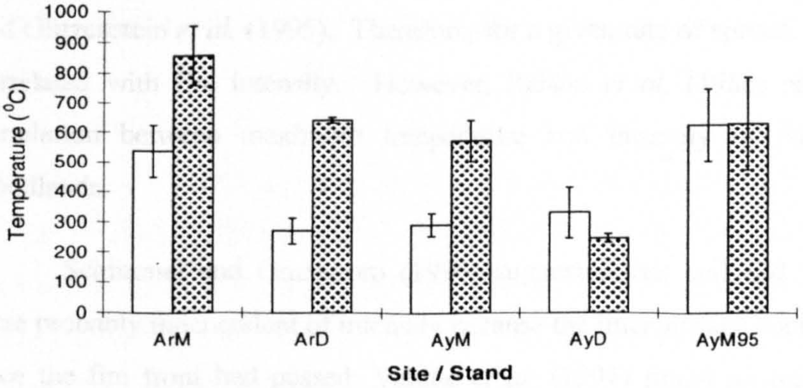
Temperatures recorded by pyrometers



Adjusted for 1 minute exposure



Adjusted for 2 minute exposure



Under an exposure time of 1 minute the maximum above - ground temperatures would be increased by around 50% (Fig 3.5). For example, temperatures in the high fuel load treatment at the Arne mature stand would be increased from approximately 600 to 900°C. The mean temperatures in both treatments in the 1995 fires at the Aylesbeare mature stand would be around 700°C. The adjustment in the two minute exposure scenario (Fig. 3.5) gave temperatures that were slightly lower than in the one minute exposure.

3.4. Discussion

3.4.1. Temperature and Intensity

Fire temperature and intensity (expressed as heat released per unit area) were dependent on fuel load consumed. All stands in the 1994 fires except the Aylesbeare degenerate stand had significantly higher temperatures in the high fuel load treatments than in the low fuel loads and temperatures were positively correlated with fuel load consumed. Sparling & Smith (1966) and Stinson & Wright (1969), also found relationships between vegetation biomass and fire temperature. The vegetation fuel load was not manipulated in the 1995 fires and the temperatures between the two paraffin treatments were extremely similar. Therefore the addition of 0.125 l /m^2 (0.75 l per plot) of paraffin was unsuccessful as a substitute for vegetation fuel load.

Pyrometer temperatures at all vertical postions in the 1994 fires were positively correlated with the pecentage of available fuel consumed, vegetation fuel load consumed and heat released per unit area. This is in agreement with Trollope (1984) and Glitzenstein *et al.* (1995). Therefore, for a given rate of spread, fire temperature is correlated with fire intensity. However, Raison *et al.* (1986) reported a negative correlation between maximum temperature and intensity in Australian Eucalypt woodlands.

Schimmel and Granstrom (1996) suggested that soil and litter temperatures were probably independent of intensity because the litter surface continued to smoulder once the fire front had passed. Valette *et al.* (1994) found no relationship between intensity and maximum soil temperatures, although intensity did affect the duration of maximum temperatures in the soil.

The calculation for heat released per unit area means that this quantity is determined predominantly by fuel load consumed. Fire intensity also incorporates the rate of energy release, which was not measured in this study. The rate of spread of fires is thought to be a function of wind speed and fuel distribution (Kayll, 1966; Hobbs and Gimingham, 1984a; van Wilgen, Le Maitre and Kruger, 1985; Marsden-Smedley and Catchpole, 1995).

Fire temperature is also likely to be influenced by these factors. Whittaker (1961) and Kenworthy (1963), working on heath fires in Scotland, stressed wind speed as the principal environmental variable affecting fire temperature but it is unlikely to be a major factor in this study because the areas burnt were small and wind speed was moderate and fairly constant. Other workers have emphasised the role of weather variables, especially air temperature and relative humidity. These have more indirect effects on temperature and intensity via vegetation characteristics. For example, moisture contents of vegetation, litter and soil vary with relative humidity (Trollope, 1984). Air temperature modifies the temperature of the fuel and hence the quantity of heat required to raise it to ignition point (Brown and Davis, 1973). It also affects relative humidity and moisture losses by evaporation (Luke and McArthur, 1978). By burning on the same day, these factors were almost constant between fires and the small differences between stands would not be expected to be of importance.

Vegetation structure may be an important factor affecting fire temperatures (Kayll, 1966; Sparling and Smith, 1966; Hobbs and Gimingham, 1984a; Hobbs, Currall and Gimingham, 1984; Gibson, Hartnett and Merrill, 1990). Hobbs and Gimingham (1984a) found that maximum temperatures increased with stand age but were lower in very old stands because bushes that had collapsed from the centre altered the fuel structure. This effect has been enhanced in the first experiment of this study by the removal of some bushes to decrease fuel load, so the lower temperatures recorded in the low fuel load treatment at the degenerate stands may be due not only to the lower fuel load but also to the change in fuel distribution. Similarly, addition of material to building-mature heath produced a more homogeneous vegetation structure by filling in any gaps in the canopy with cut material and may explain the higher temperatures in these fires. In this study, temperatures seemed to be affected more by fuel load than by fuel distribution. Temperatures in fires of similar fuel loads in different stands were not significantly different between stands in the high fuel load treatments at Arne or the low fuel load treatments at Aylesbeare. Only the soil surface temperature in the low fuel load treatments at Arne was significantly different between stands. However, the temperature of the high fuel load treatment in the mature stand at Aylesbeare was significantly higher than that in the degenerate stand. Therefore, fuel structure may have influenced temperature here. It is of note that the mean heat released per unit area was also greater in this treatment at the mature stand because a significantly greater proportion of the vegetation was consumed by fire.

Hobbs, Currall and Gimingham (1984) emphasised the importance of considering the range of temperatures recorded. Variation within plots was not examined in this study because there were only three pyrometers per plot. However, vegetation structure and density was undoubtedly heterogeneous within plots and the temperature recorded by a pyrometer would depend on the fuel immediately surrounding it.

3.4.2. Comparison of 1994 and 1995 fires

The temperatures recorded in the 1995 fires at the Aylesbeare Mature stand were noticeably hotter at the litter surface than fires at the same stand in 1994, although soil surface and above-ground temperatures were quite similar. The difference may be due to different moisture contents of the fuel and weather conditions before and on the day of burning. The fuel load consumed was similar in both years, implying that the heat released per unit area was also similar.

There was a discrepancy between the soil surface temperatures measured by the thermocouples and pyrometers in the 1995 fires. The pyrometers recorded a mean of 80°C in the added paraffin fires and 24°C in the no added paraffin fires whereas the thermocouples recorded approximately 16°C in both treatments. The most likely explanation for this difference is that the thermocouples were positioned just below, instead of on, the soil surface.

In contrast, thermocouples recorded higher temperatures than the pyrometers in the above-ground position. Maximum fire temperatures were about 600°C according to thermocouples and around 450°C according to pyrometers. This difference may be due in part to the positions of the thermocouples with respect to the pyrometers. Pyrometers only protuded 14cm above the litter surface. It is possible that maximum temperatures were above this height.

3.4.3. Comparison of fire temperatures with previous work

The maximum above ground temperatures generated in the 1994 fires were in the same range as those recorded in heathland fires by Whittaker (1961), Kenworthy (1963), Hobbs and Gimingham (1984a) and Hobbs, Currall and Gimingham (1984), but tended to be somewhat cooler overall. The temperatures at the Aylesbeare degenerate stand were exceptionally low, with a maximum temperature in the high fuel load treatment of only 204°C and a mean of 155°C. However, the higher temperatures recorded by thermocouples in the 1995 fires at Aylesbeare were more similar to those in the literature.

The litter surface temperatures were considerably lower than those reported in the literature. Whittaker (1961) recorded ground surface temperatures of between 300-500°C. Hobbs and Gimingham (1984a) and Hobbs, Currall and Gimingham (1984) noted that temperatures on the ground differed little from canopy temperatures. In this study, the litter surface temperatures of both the 1994 and 1995 fires were lower than those recorded above ground, although the difference was more exteme in the 1994 fires than in the 1995 fires.

Mean litter surface temperatures in the 1995 fires at the Aylesbeare mature stand were nearly 300°C. The highest mean litter surface temperatures in the 1994 fires were about 160°C in the high fuel load treatment at the Arne mature stand. The highest melting-point paint that melted at any of the stands in this year was 704°C. Surface temperatures at Aylesbeare were lower than those at Arne at around 90°C at the mature stand and only 22°C at the degenerate stand. This may be due to the differences in vegetation structure at the two sites. At Arne, bushes tended to be growing upright and only spread out when degenerate. At Aylesbeare, layering occurred at both stands and many stems were growing horizontally, becoming incorporated into the litter layer. The samples for vegetation moisture contents were taken from near the top of the canopy and it might be expected that the moisture content of vegetation close to the ground and sheltered from the wind would be more similar to that of the litter rather than vegetation in the canopy. Therefore, the dense layered vegetation would have increased the fuel load close to the ground but the damp vegetation and stems probably insulated the litter layer.

The mean soil temperatures were lower than those at the litter surface in both the 1994 and 1995 fires, indicating that the litter layer insulated the soil from elevated temperatures. The litter layer was deeper at the degenerate stands than at the mature stands so temperatures at the soil surface were lower at these stands at both sites. Hobbs and Gimingham (1984a) found that the highest temperature 1cm beneath the surface was 70°C. The maximum recorded in the 1994 fires was higher than this at 204°C in the high fuel load treatment at Arne Mature. The mean soil surface temperature however, was around 65°C at this stand and less than this in all other treatments and stands. Biochemical processes are disrupted at 60°C and partial sterilisation of the soil occurs (Raison *et al.*, 1986). *Calluna* seeds are killed at 200°C (Whittaker and Gimingham, 1962). Therefore the rootstock, seed and microbial processes in the soil are unlikely to be adversely affected.

3.4.4. Comparison of fire intensities with previous work

Fire intensity itself was not estimated in this investigation due to the difficulty in measuring the fires' rates of spread. The value for heat released per unit area measured here is equivalent to the available heat energy described in Hobbs and Gimingham (1984a). Their values for mature and degenerate stands were 27-40 MJm^{-2}. These fall within the range of estimates in this investigation, where mean intensities of between 17.8 and 50.2 MJm^{-2} were recorded. The Aylesbeare treatments which had fuel load manipulated i.e. the high fuel load fires at the mature stand and the low fuel load fires at the degenerate stand had values somewhat higher and lower respectively.

The effect of litter consumption on heat released is unknown. The estimates for litter biomass before and after burning were so variable that litter was not included in the calculation. If litter was consumed in the experimental fires the heat input to the soil would be increased (Albini, 1976). Therefore the heat released per unit area may be under-estimated. However, Hobbs and Gimingham (1984a) also did not consider litter consumption in their calculations of intensity, so these results are comparable.

Hobbs and Gimingham (1984a) found that intensity increased with stand age, except in the oldest degenerate stands where rates of spread were slow due to the heterogeneity of the vegetation structure. At the Aylesbeare degenerate stand, where half the biomass was removed to create the low fuel load treatment, the heat released was less than the low fuel treatment in the mature stand because a smaller proportion of the vegetation was consumed by fire. This suggests that, at Aylesbeare at least, vegetation structure as well as biomass may have had an effect on heat released. The amount of vegetation added or removed at Arne was less than at Aylesbeare so did not have such a strong impact. Since fire temperatures were highest in the most homogeneous treatments (mature stands, high fuel load) and lowest in the most heterogeneous treatments (degenerate stands, low fuel load), it seems that fire temperatures may be a reasonable reflection of fire intensity.

3.4.5. Adjustments to fire temperatures under different exposure time scenarios

If the Tempilaq° paints and Tempilstiks° took longer to melt at their specified melting points than the duration of that temperature, then the pyrometers may have under-estimated the true temperature. The response of the pyrometers may also depend on the conduction properties of ceramic tiles or the large surface area of the tiles. Different parts or sides of the tiles may have been exposed to different temperatures and so the temperature recorded will be dependent on the orientation of the tiles. The data obtained from the third experiment on paint sensitivities can be used to suggest temperatures that may have occurred, depending on how long pyrometers were exposed to elevated temperatures. Since the exposure time was not measured for individual pyrometers, the recorded data should not be replaced by adjusted data, it can only be used to suggest a range of possibilities.

Soil temperatures could be considerably higher than recorded if elevated temperatures in the soil lasted three or four minutes. The duration of the temperature pulse in the soil is difficult to estimate, since the amount of heat transferred depends on the duration of high temperatures above the ground surface (DeBano, Dunn and Conrad, 1977) as well as the degree of insulation afforded by the litter layer. Work by Valette *et al.* (1994) on the humic layer beneath pine litter showed that the effectiveness of the humus as an insulator is determined by its depth and moisture content. The litter and humic layers in heathland would be expected to behave in a similar fashion. Furthermore, the exposure time of these slightly elevated temperatures could have been considerably more than 4 minutes. Smith and Sparling (1966) recorded ground level temperatures above 100°C for longer than 8 minutes below a maximum temperature of 545°C of less than 20 sec duration in Canadian Jack Pine Barren. In North Carolina pine forests Swift *et al.* (1993) measured flame temperatures of 800°C lasting for less than two minutes, accompanied by a prolonged 10 minute heat pulse of 60°C at a depth of 5cm into the soil. Given that litter did remain after burning and exposure times of longer than 4 minutes were likely, the recorded temperatures probably are a good estimate.

When burning, the litter surface was often observed to smoulder after the flame front had passed. Therefore it seems reasonable to adjust the recorded temperatures to those that may be expected under a 3 or 4 minute exposure. Litter temperatures in this study would then be higher than those recorded by Kayll (1966) but not as high as those of Hobbs and Gimingham (1984a) or Hobbs *et al.* (1984). Even under the 3 minute exposure time scenario, temperatures would not approach those recorded above ground.

The maximum above ground temperatures were likely to be under-estimated because of the brief duration of flaming combustion at any particular position. The mean duration of temperature above 400°C recorded by the data logger in the 1995 fires was about 1.5 minutes. Kenworthy (1963) and Hobbs and Gimingham (1984a) measured durations of usually less than 1 minute and Whittaker (1961) reported that temperatures of 300 - 500°C were maintained for less than 2.5 minutes. Under exposure times of 1 or 2 minutes the maximum above ground temperatures were more likely to be between 360 and 600°C in the 1994 low fuel load fires and 330 - 890°C in the high fuel load fires. The estimated maximum of the 1995 fires would increase from about 450°C to 680°C, a value much more similar to the mean maxima recorded by thermocouples. These temperatures are similar to those recorded by other workers such as Whittaker (1961) and Hobbs and Gimingham (1984a).

3.4.6. Conclusions

This study has demonstrated that, in general, increasing the vegetation fuel load causes hotter and more intense fires which remove more of the above-ground biomass. Therefore it may be desirable to add vegetation as fuel in management fires if the moisture content of the fuel load is high or if fuel distribution within the stand is heterogeneous. The fire intensities in these management fires were not high enough to remove all the litter, so the soil seed bank and rootstocks were probably protected from high temperatures.

Although the pyrometers used were inaccurate due to the response times of the paints and crayons, they were adequate to provide comparisons between fires. Fire temperature and intensity may affect the post-fire vegetation recovery. Subsequent chapters describe vegetative regeneration and seedling demography in relation to the fire temperature treatments.

CHAPTER FOUR

The effect of burning on nutrients and seed banks in the soil and litter

4.1. Introduction

The effect of burning on the soil and litter of heathlands may have repercussions on subsequent seedling establishment and vegetative regeneration. Fire temperature and intensity may affect both the seed bank[2] and the available nutrients in the soil and litter. The seed bank in the soil and litter provides a source of propagules for response to a drastic disturbance such as fire (Miller and Cummins, 1987; Ferrandis, Herranz and Martínez-Sánchez, 1996). The flux of nutrients after burning may affect both seedling establishment and resprouting from stem bases.

The seed bank may be either depleted or increased by fire, depending on fire temperatures and exposure times. Whittaker and Gimingham (1962) found that temperatures of more than 200°C killed *Calluna* seeds. Temperatures of 120°C stimulated germination at exposure times of less than 25 seconds, but germination rates rapidly declined at exposure times greater than this. However, subsequent work by Mallik and Gimingham (1985) and González-Rabanal and Casal (1995) found no such effect. Elevated temperatures may stimulate germination of other heathland species (van de Venter and Esterhuizen, 1988; González-Rabanal and Casal, 1995). There was no effect of fire on the total seed bank in chaparral because the responses of species counter-balanced (Zammit and Zedler, 1988).

Seed banks existing beneath heathland vegetation have been researched with respect to restoration (Putwain, Gillham and Holliday, 1982; Pywell, Putwain and Webb, 1997), succession (Hester, Gimingham and Miles, 1991) and turf-cutting (Traynor, 1995). *Calluna* forms a large persistent seed bank of long-lived seeds (Thompson and Grime, 1979, Hill and Stevens, 1981; Granström, 1988; Miller and Cummins, 1987; Willems, 1988; Thompson, Bekker and Bakker, 1997). The spatial

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[2] The population of viable dormant seeds that accumulates in and on soil (Begon, Harper and Townsend, 1990)

distribution of the seed bank is patchy, because seeds are deposited close to the parent plant (Welch, Miller and Legg, 1990; Legg, Maltby and Proctor, 1992). The acidity of heathland soils results in a depauperate soil fauna and the development of distinct horizons due to lack of mixing. Therefore seeds accumulate in the upper soil horizons. Between 80 and 90% of the *Calluna* seed bank is concentrated in the uppermost 4 - 6 cm (Putwain *et al.*, 1982; Mallik, Hobbs and Legg, 1984; Miller and Cummins, 1987; Legg *et al.*, 1992;).

The effects of fire temperature and intensity on the nutrient contents of soil and litter are complex. During burning, nutrients in the vegetation are either lost from the system in smoke or deposited in ash (Gimingham, 1972). The quantity of nutrients lost in smoke increases rapidly as fire temperature rises above 300°C, particularly of those which form volatile compounds (carbon, nitrogen and sulphur) (Kenworthy 1963, Allen, 1964; Evans and Allen, 1971; DeBano and Conrad, 1978). Allen (1964) recorded more than 50% losses of carbon, nitrogen and sulphur in fire temperatures of 550 - 650°C, and losses of nitrogen approached 80% in fires of 800 - 825°C. In artificial fires of unknown temperatures, Chapman (1967) reported up to 95% of nitrogen lost in smoke, compared with 20 - 30% of the other nutrients.

Nutrients are leached from the ash through the soil at different rates and the capacity of the soil to retain nutrients may vary. Fine ash particles may be washed into spaces in the surface layers of the soil, impeding drainage and increasing run-off (Allen, 1964). The degree of retention of nutrients by soils depends on the thickness of the organic layer (Allen, Evans and Grimshaw, 1969). Therefore podsols experience more rapid leaching than peats (Gimingham, 1972). The rate at which nutrients are leached through the soil depends on the structure, compactness and porosity of the soil and the rate of leaching may influence the degree of adsorption by the soil particles (Allen, 1964). For example, the phosphorus-adsorption capacity of Dorset heathland soils is low (Chapman, Rose and Basanta, 1989), so the soil is unable to retain all the phosphorus that is liberated on burning (Chapman, Rose and Clarke, 1989). Phosphorus tends to remain in an insoluble form in the ash, whereas potassium readily forms soluble compounds which are rapidly leached through the soil profile (Allen, 1964).

There may be further loss of nutrients in the days following fire if ash is removed by wind or washed along the soil surface by rain, depositing nutrients elsewhere (Allen, 1964). The effect of burning on nutrient status may be temporary, because most nutrients, except nitrogen and phosphorus, may be soon replaced by nutrients in precipitation (Robertson and Davies, 1965; Chapman, 1967; Evans and Allen, 1971).

This chapter describes the effect of burning different fuel loads on the size of seed banks and three nutrients (phosphorus, potassium and calcium). The aim of the work was not to provide a detailed description of nutrient and seed dynamics, but to present a 'snapshot' of the soil nutrient and seed bank status before and after burning.

4.2 Methods

4.2.1 Burning

Experiment 1. 1994 Fires

Mature and degenerate stands of vegetation were selected at two sites: Arne in Dorset and Aylesbeare in Devon (Chapter Two). Twelve plots of 5 x 5 m were laid out in a strip at each stand separated from one another by 3m to minimise ash drift. A randomised block design was used, with four replicate blocks of two burning treatments plus unburnt controls at each stand. The treatments were to burn high and low fuel loads of vegetation. Burning was carried out in March, 1994. The methods of vegetation manipulation and burning are described in Chapter Three. Temperatures were recorded with pyrometers consisting of temperature sensitive paints in strips on tiles.

Experiment 2: 1995 Fires

Only the Aylesbeare Mature stand was used for the second experiment in March 1995. A strip of twelve plots of 3m x 2m was set up adjacent to the plots burnt in 1994. A randomised block design of two treatments plus unburnt controls was employed. The two burning treatments were to burn plots sprayed with 0.75 l of paraffin and plots with no added paraffin (Chapter Three). Two methods of temperature recording were used: pyrometers as described above and thermocouples attached to a data logger.

4.2.2. Seed Banks

One soil sample per plot of the 1994 experiment was taken before and after burning at all stands (12 samples per stand). Pre-burn sampling was carried out in December 1993 and post-burn sampling in May 1994. Two samples per plot were taken before and after burning at the Aylesbeare mature stand in 1995. The pre-burn samples were taken a week before burning in March 1995 and the post-burn samples the same day as burning.

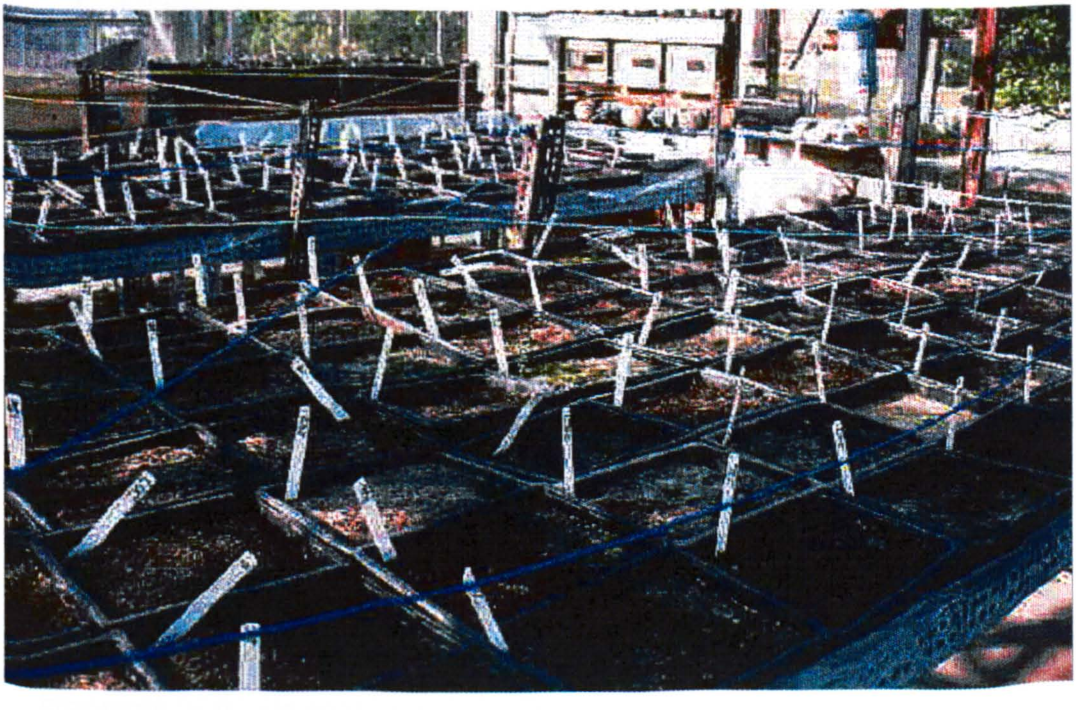
Intact blocks of soil of 150 x 150 mm were dug to a depth of about 100 mm. Samples were stored in the dark at about 4°C for one week. In the laboratory, soil blocks were trimmed to 100 x 100 mm and sectioned into litter, 0 - 20 mm depth (humic) and 20 - 60 mm (mineral) components. These sections were air-dried at 20°C for two weeks and then sieved through a 2mm mesh to remove stones and roots. Sieved samples were weighed and sub-samples of approximately 225 cm^3 removed from the soil samples and 100 cm^3 from the litter samples. The weights of the sub-samples were used to calculate the percentage that had been sub-sampled from the original samples.

Seed trays (160 mm x 204 mm x 50 mm) were prepared with a thin layer of gravel and then 4 mm of sterile sand for the soil samples and a 1:1 mixture of sand and Irish moss peat for the litter samples. Samples were spread thinly on top (Plate 4.1). There were two control trays per bench in the greenhouse, one of sand and one of the sand and peat mixture. Samples were positioned randomly on capillary matting on benches in the greenhouse (Plate 4.2) and were watered from below with trickle irrigation. The frequency of watering depended on weather, but tended to be about once a week in the winter and three times a week in the summer.

Emerged seedlings were counted and removed every two months. After six months, samples were completely stirred to encourage further germination and the

Plate 4.1. *Calluna* seedlings in seed bank sample

Plate 4.2. Randomised seed bank samples in greenhouse



trays re-randomised. Samples were left for one year when there was no further germination.

4.2.3. Soil and ash / litter nutrients

Two soil samples per plot were taken before and after burning in 1994. The pre-burn samples were taken in February 1994 and the post-burn samples the day after burning in March 1994. The samples from the 1995 experiment at Aylesbeare were taken a week before burning in March 1995 and the post-burn samples were taken on the same day as burning. Only the humic layer was sampled, so samples from the mature stands were taken to about 2 cm depth and samples from the degenerate stands to about 4 cm depth. Two randomly -positioned samples of ash and litter per plot were also taken after burning.

The pH of fresh soil samples was determined using the method described in Appendix One. All samples (soil and ash / litter) were air-dried at 30°C and sieved through a 2mm mesh to remove roots and stones.

The concentrations of phosphorus (P), calcium (Ca) and potassium (K) in soil and ash / litter samples were determined using methods described in Allen (1989). The extraction procedures were modified for soils of low nutrient contents using methods in the Handbook for Analytical Procedures (University of Liverpool, unpublished). Ash and litter samples were digested following the mixed acid procedure for plant material described in Allen (1989).

The method of determining each nutrient is described in Appendix Two. An extraction 'blank' (filtered reagents) and a reference soil (GD2 from the Chemical Service at ITE Merlewood) were tested with each batch of soils. Nutrient concentrations are given in mg 100 g^{-1} soil.

4.2.4. Data Analysis

Both seed bank and soil nutrient data were checked for normality and homogeneity of variances and log-transformed if necessary. Balanced ANOVAs were performed on pre-burn data to check there was no significant variation between plots due to chance. Fuel load treatments were compared with controls after burning by balanced ANOVA and least significant differences (LSD) using Bonferroni's Adjustment were calculated to test comparisons between means.

4.3. Results

4.3.1. Burning

Experiment 1. 1994 Fires

The results of burning high and low fuel loads at mature and degenerate heath at both sites are described in Chapter Three (Table 3.5). Fires in the high fuel load treatments were significantly hotter and more intense than the fires in the low fuel load treatments. The Aylesbeare degenerate stand was the exception, where all the fires were comparatively cool. Above-ground temperatures were higher than the temperatures on the litter surface, with maxima of 400 - 500°C in high fuel load fires. Litter surface temperatures were very variable. The highest mean litter surface temperature was 163°C, recorded in high fuel load fires at the Arne mature stand.

Experiment 2: 1995 Fires

There was no significant difference in mean temperature between the two burning treatments. Fire temperatures recorded by pyrometers and thermocouples are shown in Table 3.10 in Chapter Three. Pyrometers recorded mean litter surface temperatures of 200 - 300°C and above -ground temperatures of about 450°C. Thermocouples in the canopy recorded mean temperatures of about 600°C.

4.3.2. Seed banks

Contaminants such as *Salix* spp., *Epilobium tetragonum*, *Oxalis acetosella* and *Buddleja davidii* germinated in all the samples and in the control trays. All species were found growing either in or around the greenhouse, and were removed regularly from the samples without counting. *Betula pubescens* and *B. pendula* may have been present in the seed bank samples, but estimates could not be made due to contamination that occurred in the greenhouse. Seedlings of these species emerged in control trays as well as in the samples and wind-borne seeds were observed on several occasions.

Analyses of variance on the size of the seed bank present before burning showed no significant differences amongst experimental plots, indicating uniformity prior to burning treatments.

Experiment 1: 1994 Fires

Arne

The seed bank at both stands at Arne was dominated by *Calluna* (Fig. 4.1). Over 90% of the seedlings that emerged from samples taken from the mature stand were *Calluna* (Table 4.1). There were approximately equal quantities of *Erica cinerea* and *Erica tetralix* seed in samples taken from the degenerate stand, and both were more common in the mineral soil than in the litter or humus (Table 4.1).

Table 4.1. Percentage contribution (± 1 SE) of species to the seedbank at each stratum and total number of seeds m^{-2} before burning at Arne. Values are mean percentages of twelve plots ± 1 SE

		Mature			**Degenerate**	
Species	**Litter**	**Humic**	**Mineral**	**Litter**	**Humic**	**Mineral**
Calluna	99.61 ± 0.23	99.08 ± 0.37	95.24 ± 3.64	92.96 ± 3.56	93.01 ± 2.29	79.71 ± 8.32
Erica cinerea	0.18 ± 0.18	0.16 ± 0.11	4.76 ± 3.64	3.19 ± 2.40	3.36 ± 2.02	10.41 ± 6.58
Erica tetralix	0.12 ± 0.08	0.73 ± 0.38	0.00 ± 0.00	3.69 ± 2.97	3.63 ± 1.78	5.56 ± 3.47
Ulex minor	0.05 ± 0.05	0.03 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.21 ± 0.14	1.45 ± 1.45
Agrostis curtisii	0.05 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.09	0.00 ± 0.00	1.81 ± 1.23
Total number of seeds m^{-2}	11844 ± 1346	15471 ± 4525	334.6 ± 112.2	21502 ± 3866	19351 ± 2394	2879 ± 1126

The seed bank of the degenerate stand was larger than that of the mature stand, but only the mineral strata were significantly different (two-sample t-test, T= 4.22, $P < 0.001$, 14 df). The mean total seed bank at the mature stand (all species and strata) was 43732 seeds m^{-2}, compared with 27649 m^{-2} at the degenerate stand. Most (98.84 %) of the Calluna seed bank was concentrated in the litter and humic layers at both stands. There was more seed m^{-2} in the humic stratum than in the litter at the mature stand, but the reverse was true of the degenerate stand. However, the litter

Fig. 4.1. *Calluna* seed bank at Arne before burning. Values are means ± 1 SE.

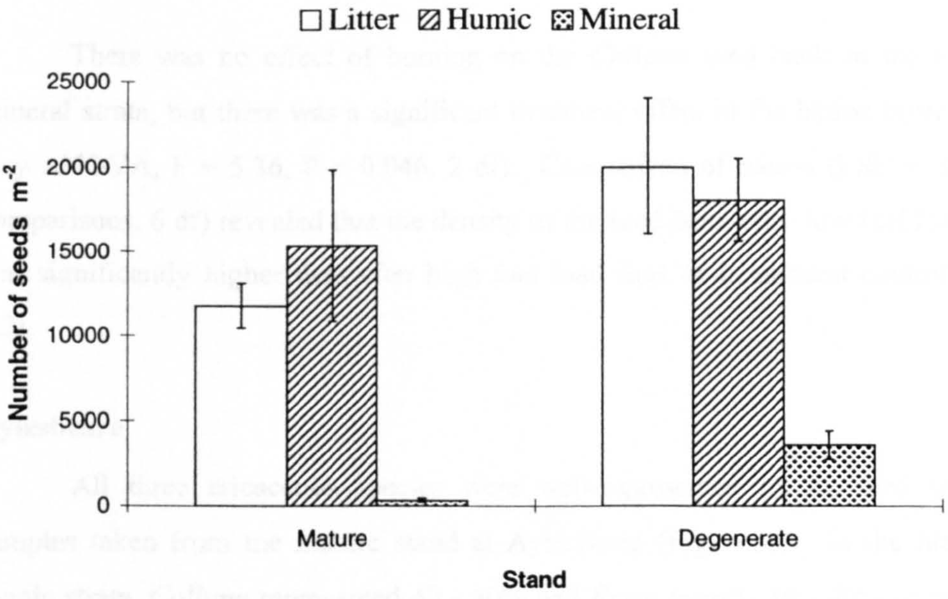
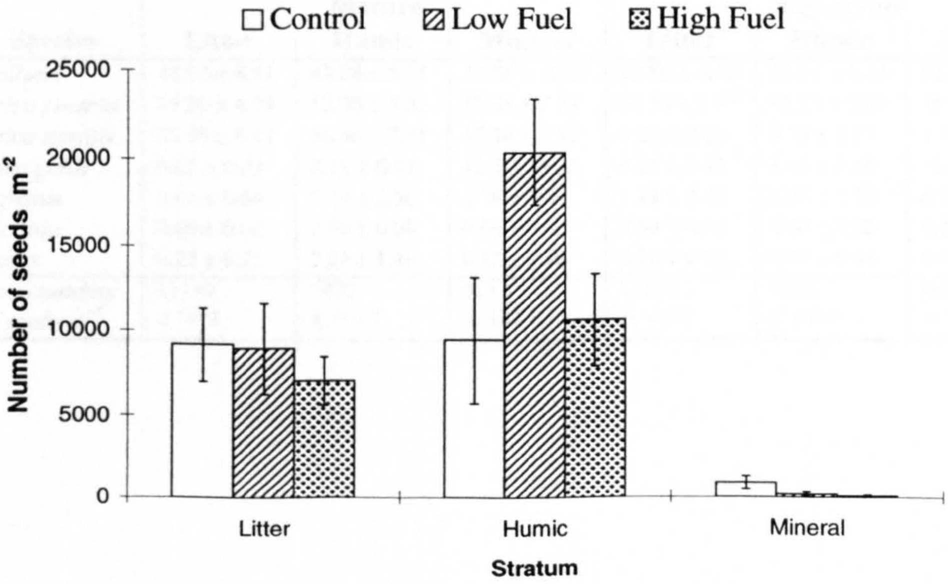


Fig. 4.2. *Calluna* seed bank at the Arne mature stand after burning. Values are means ± 1 SE.



layer was about 4 cm deep at the degenerate stand, compared with less than 2 cm at the mature stand.

There was no effect of burning on the *Calluna* seed bank in the litter or mineral strata, but there was a significant treatment effect in the humic layer (Two-way ANOVA, F = 5.36, P = 0.046, 2 df). Comparison of means (LSD = 8366, 3 comparisons, 6 df) revealed that the density of the seed bank after low fuel load fires was significantly higher than after high fuel load fires or in unburnt controls (Fig. 4.2).

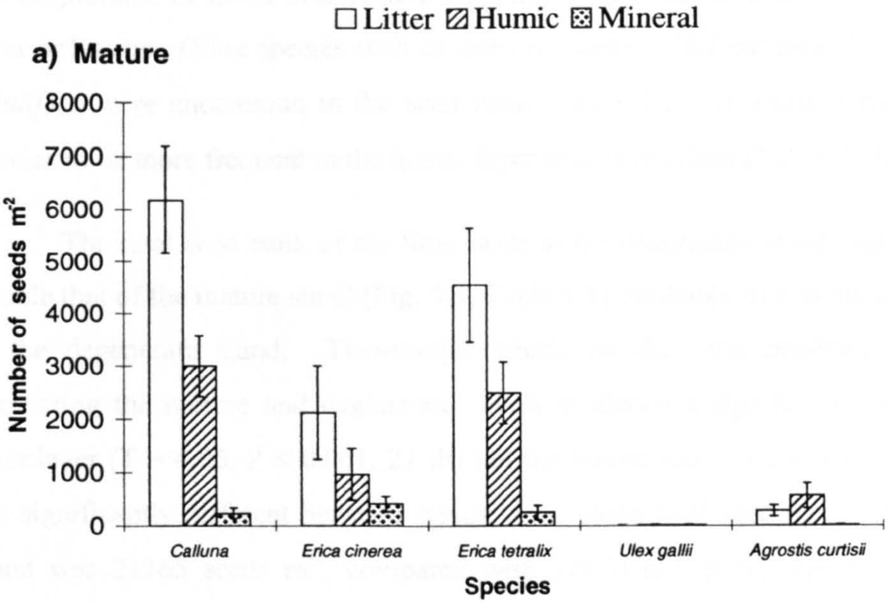
Aylesbeare

All three ericaceous species were well-represented in the seed bank of samples taken from the mature stand at Aylesbeare (Fig. 4.3a). In the litter and humic strata, *Calluna* represented 40 - 50% and *Erica tetralix* 30 - 40% of the total seed bank (Table 4.2).

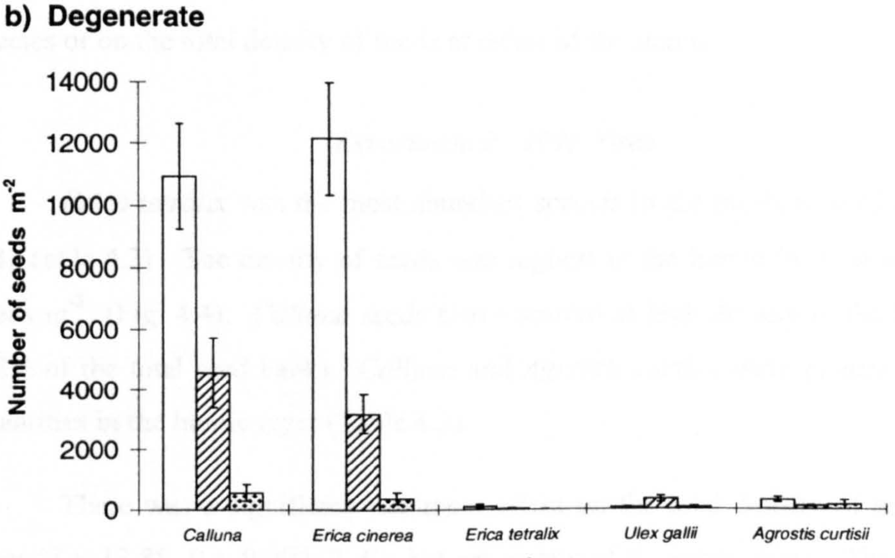
Table 4.2. Percentage contribution (± 1SE) of species to the seedbank at each stratum and total number of seeds m^{-2} before burning at Aylesbeare. *Agrostis* = *Agrostis curtisii*, *Molinia* = *Molinia caerulea*, *Carex* = *Carex pilulifera*

		Mature			**Degenerate**	
Species	**Litter**	**Humic**	**Mineral**	**Litter**	**Humic**	**Mineral**
Calluna	48.92 ± 6.51	41.88 ± 5.73	32.44 ± 10.19	47.86 ± 6.12	52.91 ± 5.43	62.84 ± 10.84
Erica cinerea	15.36 ± 4.94	12.36 ± 5.52	37.08 ± 7.96	51.53 ± 6.09	45.99 ± 5.32	35.14 ± 11.15
Erica tetralix	32.79 ± 6.47	36.46 ± 7.31	15.36 ± 5.90	0.37 ± 0.28	0.33 ± 0.27	1.11 ± 1.01
Ulex gallii	0.03 ± 0.03	0.11 ± 0.11	12.5 ± 10.20	0.27 ± 0.09	8.78 ± 4.79	11.53 ± 9.02
Agrostis	2.04 ± 0.64	7.14 ± 2.96	1.79 ± 1.46	1.43 ± 0.40	1.54 ± 0.34	6.87 ± 6.28
Molinia	0.60 ± 0.60	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Carex	0.27 ± 0.22	2.06 ± 1.46	0.83 ± 0.68	0.20 ± 0.20	0.94 ± 0.94	0.00 ± 0.00
Total number of seeds m^{-2}	13180 ± 1608	7072 ± 743.7	913.1 ± 324.1	23235 ± 1886	7855 ± 1355	980.2 ± 359.6

Fig. 4.3. Seed bank at Aylesbeare before burning. Values are means ± 1 SE.



a) Mature



b) Degenerate

The proportions of these two species were smaller in the mineral soil because the proportions of *Erica cinerea* and *Ulex gallii* were higher than they were in the litter or humus. Other species such as *Agrostis curtisii*, *Molinia caerulea* and *Carex pilulifera* were uncommon in the seed bank (Table 4.2). *A. curtisii* was the only species to be more frequent in the humic layer than in the litter (Fig. 4.3, Table 4.2).

The total seed bank of the litter layer at the degenerate stand was more than double that of the mature stand (Fig. 4.3, Table 4.2), probably due to the deeper litter at the degenerate stand. Two-sample t-tests on the total pre-burn seed bank comparing the mature and degenerate stands produced a significant value for the litter layer ($T = 4.06$, $P < 0.001$, 21 df) but the humic and mineral seed banks were not significantly different between stands. The mean total seed bank at the mature stand was 21165 seeds m^{-2}, compared with 32070 m^{-2} at the degenerate stand. *Calluna* and *Erica cinerea* were co-dominant in the seed bank at the degenerate stand (Fig. 4.3b). *Erica tetralix* was infrequent in both the seed bank and the vegetation (Chapter Two). There was no effect of burning on the seed bank of any of the species or on the total density of seeds at either of the stands.

Experiment 2. 1995 Fires

Erica tetralix was the most abundant species in the pre-burn seed bank (Fig. 4.4, Table 4.3). The density of seeds was highest in the humic layer at about 6000 seeds m^{-2} (Fig. 4.4). *Calluna* seeds also occurred at high density in the litter layer (38% of the total seed bank). *Calluna* and *Agrostis curtisii* were present in similar quantities in the humic layer (Table 4.3).

There was a significant treatment effect on the total density of seeds in the litter ($F = 13.85$, $P = 0.006$, 2 df), but not at any of the other strata. The total litter seed bank after burning was 4651 seeds m^{-2} (Table 4.3). *Erica tetralix* comprised 27% of this total, compared with 45% before burning. The seed bank of *Erica tetralix* was significantly smaller after burning than in the control plots (Fig. 4.5). However, there was no difference between the two treatments.

Fig. 4.4. Seed bank at the Aylesbeare mature stand (1995 Fires) before burning. Values are means ± 1 SE.

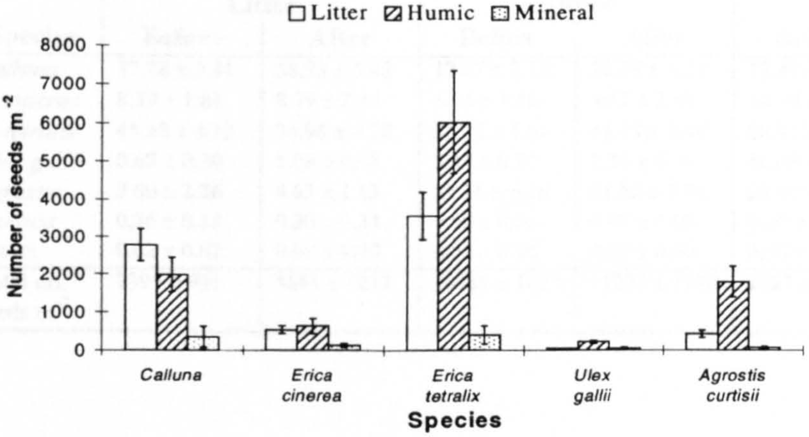


Fig. 4.5. ***Erica tetralix*** **seed bank at the Aylesbeare mature stand (1995 Fires) after burning.** Values are means ± 1 SE. -para = fires with no added paraffin, + para = fires with 0.75 l paraffin per plot.

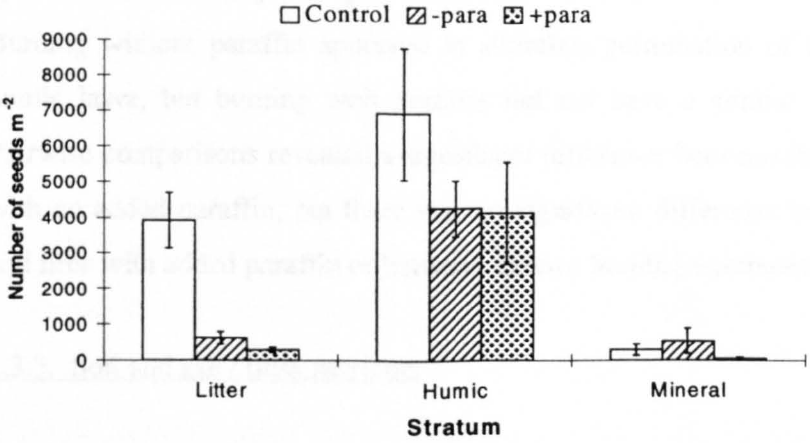


Fig. 4.6. ***Ulex gallii*** **seed bank at the Aylesbeare mature stand (1995 Fires) after burning.** Values are means ± 1 SE. -para = fires with no added paraffin, + para = fires with 0.75 l paraffin per plot.

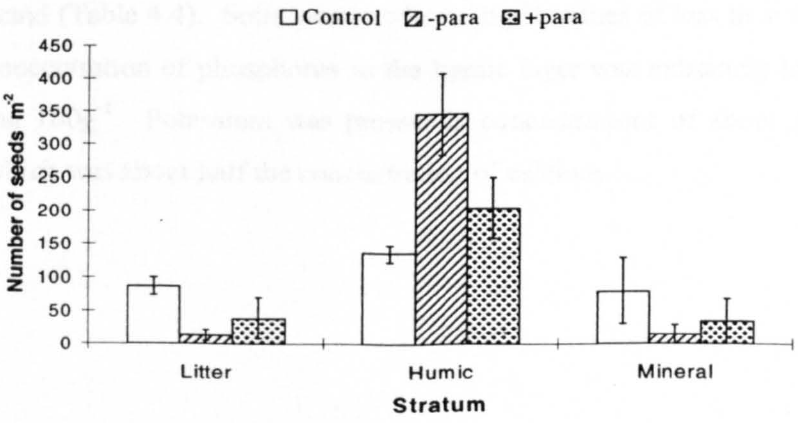


Table 4.3 Percentage contribution (± 1SE) of species to the seedbank at each stratum and total number of seeds m^{-2} before and after burning at the Aylesbeare mature stand (1995 Fires).

Species	Litter		Humic		Mineral	
	Before	**After**	**Before**	**After**	**Before**	**After**
Calluna	37.78 ± 3.41	58.23 ± 5.48	17.67 ± 2.23	22.59 ± 4.21	18.47 ± 7.58	19.70 ± 5.94
E. cinerea	8.39 ± 1.61	8.79 ± 2.44	6.04 ± 1.50	9.32 ± 2.49	16.39 ± 5.43	17.89 ± 8.53
E. tetralix	45.18 ± 4.12	26.96 ± 4.28	50.38 ± 5.64	44.13 ± 5.44	28.97 ± 7.21	34.62 ± 9.38
Ulex gallii	0.67 ± 0.30	1.08 ± 0.38	2.47 ± 0.37	2.35 ± 0.46	10.69 ± 4.56	7.10 ± 3.33
Agrostis	7.60 ± 2.26	4.63 ± 1.13	23.38 ± 6.16	21.52 ± 5.70	25.47 ± 9.24	19.58 ± 8.55
Molinia	0.36 ± 0.18	0.30 ± 0.24	0.00 ± 0.00	0.08 ± 0.08	0.00 ± 0.00	0.00 ± 0.00
Carex	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.10 ± 1.10
Total no. seeds m^{-2}	7395 ± 931	4651 ± 1012	10719 ± 1627	11235 ± 1148	1027 ± 553	821 ± 330

Ulex gallii was the only other species to show a significant response to burning, but this response was different from that of *Erica tetralix*. Seeds of this species were relatively infrequent in the seed bank (< 500 seeds m^{-2} in any strata). Burning without paraffin appeared to stimulate germination of this species in the humic layer, but burning with paraffin did not have a similar effect (Fig. 4.6). Pairwise comparisons revealed a significant difference between the control and fires with no added paraffin, but there was no significant difference between the control and fires with added paraffin or between the two burning treatments.

4.3.3. Soil and ash / litter nutrients

Soils

There were no significant differences between treatments or blocks before burning, so pre-burn data are presented as the mean values of the 12 plots at each stand (Table 4.4). Soils were acidic with pH values of less than 4 at all stands. The concentration of phosphorus in the humic layer was extremely low, at less than 0.1 mg 100g^{-1}. Potassium was present in concentrations of about 30 - 50 mg 100g^{-1}, which was about half the concentration of calcium.

Table 4.4. Pre-burn soil characteristics. Nutrients are mean values ± 1 SE (mg $100g^{-1}$) of humic layer samples (0 - 2 cm at mature stands and 0 - 4 cm at degenerate stands). pH values are for humic (H) and mineral (M) samples. Mineral samples were taken to 6 cm depth (n = 12).

Nutrient / pH	**Arne**		**Aylesbeare**		
	Mature	**Degenerate**	**Mature**	**Degenerate**	**1995 Fires**
P	0.089 ± 0.003	0.111 ± 0.004	0.063 ± 0.00	0.072 ± 0.005	0.005 ± 0.002
K	42.08 ± 2.43	55.79 ± 7.85	41.76 ± 2.71	32.84 ± 2.77	31.21 ± 4.61
Ca	91.31 ± 5.86	110.46 ± 8.94	71.34 ± 2.68	71.94 ± 7.12	96.46 ± 3.97
pH (H)	3.20 ± 0.04	3.31 ± 0.04	3.44 ± 0.04	3.57 ± 0.05	N/A
pH (M)	3.15 ± 0.03	3.11 ± 0.04	3.46 ± 0.03	3.56 ± 0.05	N/A

The pre-burn concentration of phosphorus in the plots burnt in 1995 at the Aylesbeare mature stand was significantly lower than at any other stand, but there were no significant differences among the other stands (Table 4.5). The concentration of potassium was highest at the Arne degenerate stand, and was significantly higher than at the Aylesbeare mature stand (both 1994 and 1995 plots). The concentration of calcium was relatively high at the Aylesbeare mature 1995 plots (Table 4.4), and the only significant differences were between the degenerate stand at Arne (110 mg $100g^{-1}$) and the two stands at Aylesbeare which were burnt in 1994 (about 71 mg $100g^{-1}$) (Table 4.5). Soil pH was similar between the mature and degenerate stands at both sites, but pH tended to be higher at Aylesbeare than at Arne (Table 4.4).

Table 4.5. Pairwise comparisons and LSDs of pre-burn soil characteristics using Bonferroni's adjustment, comparing sites and stands. P, K and Ca: 10 comparisons, 55 df; pH: 6 comparisons, 44df

Comparison	**P**	**K**	**Ca**	**pH (H)**	**pH (M)**
LSD	***0.015***	***18.84***	***25.35***	***0.164***	***0.157***
ArM v ArD	NS	NS	NS	NS	NS
AyM v AyD	NS	NS	NS	NS	NS
AyM v AyM95	*	NS	*	-	-
AyD v AyM95	*	NS	NS	-	-
ArM v AyM	NS	NS	NS	*	-
ArM v AyM95	*	NS	NS	-	-
ArM v AyD	NS	NS	NS	*	*
ArD v AyM	NS	NS	*	NS	*
ArD v AyM95	*	*	NS	-	-

Post-burn data are not presented because there was no effect of burning on soil nutrients in the humic layer at any stand. The pH of both humic and mineral soil was also not significantly different between treatments and controls.

Ash and litter

There were no data for the pre-burn nutrient concentrations in the litter layer, but post-burn sampling compared litter in control plots with the ash and litter in burnt plots. Nutrient concentration tended to be higher in the ash samples of burnt plots than in the litter samples of control plots (Fig. 4.7). However, only the two mature stands burnt in 1994 showed a significant treatment effect on phosphorus concentrations in ash and litter (Fig. 4.7a). Potassium and calcium concentrations were significantly affected by fire at all stands except the Aylesbeare degenerate stand (Fig. 4.7b and c).

The Arne mature stand

Pairwise comparisons (Table 4.6) showed that the concentrations of all nutrients in the ash after high fuel load fires were significantly higher than in the litter of the control plots.

Table 4.6. Pairwise comparisons between fuel load treatments and controls for nutrients in ash and litter after burning. C = control, LF = low fuel load fires, HF = high fuel load fires, -para = fires with no added paraffin, +para = fires with 0.75 l paraffin added per plot.

Stand	Comparison	P	K	Ca
Arne Mature	C *v* LF C *v* HF LF *v* HF	NS * NS	NS * *	* * *
Arne Degenerate	C *v* LF C *v* HF LF *v* HF	)) No sig. diffs.)	* NS NS	* NS NS
Aylesbeare Mature	C *v* LF C *v* HF LF *v* HF	NS * NS	NS * NS	NS * NS
Aylesbeare Degenerate		No significant differences		
Aylesbeare Mature 1995 Fires	C *v* -para C *v* +para -para *v* +para	)) No sig. diffs.)	* * NS	NS * NS

The concentrations of phosphorus and calcium were about 10 times higher after high fuel load fires than in the controls and the concentration of potassium was increased by more than 60 times. However, the concentration of phosphorus was still very low in the ash remaining after high fuel load fires, at 1.1 mg $100g^{-1}$. The concentrations of potassium and calcium were about 1200 and 4000 mg $100g^{-1}$ respectively (Fig. 4.7). There was no significant difference in the phosphorus concentration in ash deposited by high and low fuel load fires, but there was a fuel load effect on potassium and calcium (Table 4.6, Fig. 4.7). Only calcium showed a significant difference between the litter in control plots and ash of low fuel load fires.

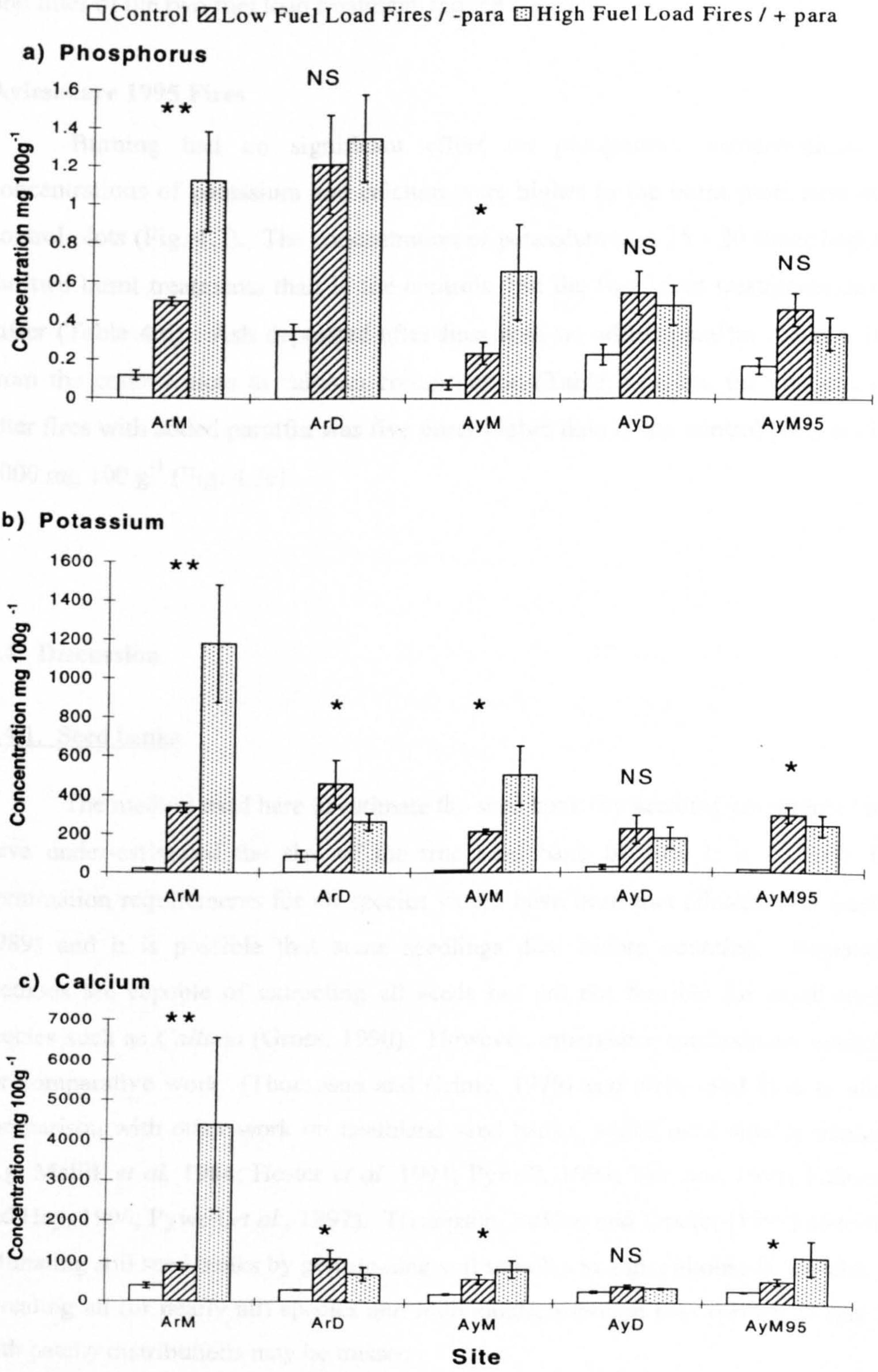
The Arne degenerate stand

Phosphorus concentrations were numerically higher in the ash deposited after burning than in the litter of control plots (Fig. 4.7a), but this difference was not quite significant ($F = 5.11$, $p = 0.051$). Both potassium and calcium were higher in the burnt plots (Fig. 4.7 b and c), but differed significantly only between the control and low fuel load treatment (Table 4.6). The concentrations of potassium and calcium in the ash remaining after low fuel load fires were about five times higher than in the control plots at about 400 and 1000 mg $100g^{-1}$ respectively. The nutrient concentrations after high fuel load fires were not significantly different from the controls.

The Aylesbeare mature stand

The concentrations of all nutrients were significantly higher in the ash deposited by the high fuel load fires than in the litter in the control plots (Table 4.6, Fig. 4.7), but there were no significant differences between the control and the low fuel load fires or between the two fuel load treatments. The concentration of potassium was 45 times higher in the ash of high fuel load fires than in the litter of controls at about 500 mg $100g^{-1}$. Phosphorus and calcium showed nine and four-fold increases respectively.

Fig. 4.7. Effect of burning on nutrient concentrations in litter. ArM = Arne Mature, ArD = Arne Degenerate, AyM = Aylesbeare Mature, AyD = Aylesbeare Degenerate, AyM95 = Aylesbeare Mature, 1995 fires. - / + paraffin refers to AyM95 only. Results of ANOVA are shown. NS = not significant, ** = 0.001 < P < 0.01, * = 0.01 < P < 0.05.



The Aylesbeare degenerate stand

There were no significant differences in the nutrient concentrations of the ash and litter of the two fuel load treatment and the controls.

Aylesbeare 1995 Fires

Burning had no significant effect on phosphorus concentrations, but concentrations of potassium and calcium were higher in the burnt plots than in the control plots (Fig. 4.7). The concentration of potassium was 15 - 20 times higher in the two burnt treatments than in the controls, but the two burnt treatments did not differ (Table 4.6). Ash deposited after fires with no added paraffin did not differ from the control plots in calcium concentration (Table 4.6), but the concentration after fires with added paraffin was five times higher than in the control plots at about 1000 mg 100 g^{-1} (Fig. 4.7c).

4.4. Discussion

4.4.1. Seed banks

The method used here to estimate the seed bank (by seedling emergence) may have under-estimated the size of the true seed bank because it is unlikely that germination requirements for all species would have been met (Baskin and Baskin, 1989) and it is possible that some seedlings died before counting. Separation methods are capable of extracting all seeds but are not feasible for small-seeded species such as *Calluna* (Gross, 1990). However, emergence methods are adequate for comparative work (Thompson and Grime, 1979) and were used here to allow comparison with other work on heathland seed banks, which used similar methods (e.g. Mallik *et al.* 1984; Hester *et al.* 1991; Pywell, 1993; Traynor, 1995; Pakeman and Hay, 1996; Pywell *et al.*, 1997). Thompson, Bakker and Bekker (1997) state that estimating soil seed banks by germinating soil samples in a greenhouse is ‘capable of revealing all (or nearly all) species and individuals, although rare species or species with patchy distributions may be missed’.

Samples were stored at 4°C for a week before air-drying, and this period of cold stratification should have increased germination (Roberts, 1981). Furthermore, conditions in the greenhouse were such that germination of all heathland species should be possible (Pakeman and Hay, 1996). Periodic disturbance of samples, fluctuating temperatures and the shallow layer of sample should all facilitate germination (Roberts, 1981; Thompson, 1986).

The relative abundances of species in the seed bank were not compared statistically with the above-ground vegetation, but it is clear that the two were very similar at all sites and stands. Studies in grasslands (Chippindale and Milton, 1934; Thompson, 1986) found no association between the seed bank and vegetation but work on heather-dominated communities in north-east Scotland (Miles, 1973) and eastern England (Pakeman and Marshall, 1997) found seed banks and vegetation were very similar.

The concentration of *Calluna* seeds in the organic layer of the soil has been studied by other workers (e.g. Moore and Wein, 1977; Putwain *et al.*, 1982; Granström, 1988; Legg *et al.*, 1992; Traynor, 1995). Granström (1988) found over 45 000 seeds m^{-2} in the top 6 cm of soil in an open heathland in Sweden, 88% of which were *Calluna*. Seeds reach the lower soil strata by percolating down with rainwater or becoming buried by the deposition of organic matter (Moore and Wein, 1977), so the depth of burial is one indication of the age of the seeds. Age affects seed viability and may account for decline in germination with increasing depth (Moore and Wein, 1977).

The estimates of the size of seed banks under mature and degenerate heath were variable. The total seed bank (all species and strata) under mature vegetation at Aylesbeare was about 20 000 seeds m^{-2}, compared with over 30 000 m^{-2} at the degnerate stand. The density of seeds at Arne was about 28 000 m^{-2} at the mature stand and nearly 44 000 m^{-2} at the degenerate stand. These differences between stands were probably due mainly to the deeper litter layers at the degenerate stands. Traynor (1995) recorded lower seed densities under mature heath at Arne (17 198 seeds m^{-2} in litter and 0 - 6 cm soil) but over 60 000 seeds m^{-2} in the same depth under degenerate heath at Aylesbeare. The mean seed bank of the top 40 mm of soil from a range of heathland sites in Dorset was 24 200 seeds m^{-2} (Pywell *et al.* 1997). Estimates of *Calluna* seed banks range from around 30 000 seeds m^{-2} under afforested heathland in Sweden (Granström, 1988; Willems, 1988) to nearly 800 000 m^{-2} in deep peat in North Yorkshire (Legg *et al.*, 1992).

The seed banks sampled before burning from the plots burnt in 1994 and 1995 at the Aylesbeare mature stand differed in species composition, despite being similar in vegetation composition. *Erica tetralix* was more frequent in the seed banks of the plots burnt in 1995 than those burnt in 1994. This difference may be due to spatial differences in the seed bank or to the conditions experienced by the samples in the greenhouse. Samples from the 1995 fires were set up in the greenhouse a year later than the 1994 samples, and may therefore have experienced different temperatures and moisture conditions.

There were very few effects of burning on the seed banks of any species. The seed bank of *Erica tetralix* in the litter layer after the 1995 fires at the Aylesbeare mature stand was significantly depleted by burning. There was no difference between the two treatments (+ / - paraffin), but this is to be expected since there was no significant difference in temperature between the two treatments (Chapter Three). *Erica tetralix* seeds may be killed at lower temperatures than other heathland species, since no other species were similarly affected.

The seed bank of *Ulex gallii* also showed a response to burning in this experiment, but only in the no added paraffin treatment. This treatment appeared to stimulate germination in the humic layer. A similar response was shown by *Calluna* in the humic layer after the low fuel load fire treatment at the Arne mature stand in 1994. There is no logical explanation for this response, because any stimulation of germination would be evident in the litter layer as well.

Depletion of seed banks by burning has been reported by Pierce and Cowling (1991), from the South African fynbos and Cancio *et al.* (1992) from Galician heathlands, where approximately 30% of seeds were destroyed by fire. However, Mallik *et al.* (1984) found a significant increase in the number of *Calluna* and *Erica cinerea* germinating after burning compared with before burning. They suggested this was due to elevated temperatures breaking dormancy. A similar effect was not noted in this study.

It appears that the quantity of litter (if any) ignited by the management fires in this study was not sufficient to have an impact on the seed bank contained within it. Even if a significant quantity of litter had been removed, the seed bank of ericaceous species in the humic soil is so large that there would be ample propagules for regeneration (Moore and Wein, 1977; Mallik *et al.*, 1984). Welch *et al.* 1990 estimated that perhaps only 10 - 20% of seedlings in the top 5 cm of heathland soil would be exposed to light after a disturbance such as fire, so the initial seedling density may be considerably less than might be expected from the size of the seed bank. A study of chaparral soil seed banks by Keeley (1977) reported that over 99% of the stored seeds did not result in seedlings. There was also a surplus of propagules available for regeneration in this study, because the density of seedlings that appeared after fire (Chapter Six) was less than the density of seed present in the seed bank.

4.4.2. Soil and ash / litter nutrients

The concentrations of calcium and potassium in the humic layer before burning are similar to those found at the same sites by Traynor (1995) and at other sites in Dorset by Pywell (1993). These workers reported phosphorus concentrations in the top 2 cm of soil of about 2 mg 100 g^{-1}. This study found concentrations of less than 0.1 mg 100 g^{-1}. The reasons for this difference are not clear, because the same extraction procedures were used in all studies.

Nutrient concentrations in the humic soil showed no immediate effect of burning. However, the humic layer may show a delayed response to fire as nutrients in the deposited ash leach downwards. This effect may be short-lived as nutrients leach into the mineral soil. The initial increase in nutrients in the organic layer after fire in jack-pine barren, Canada was not observed 15 months later (Smith, 1970). The degree of retention by the soil and leaching rates vary between nutrients (Allen, 1964). In the absence of measurements of leaching rates or a chronological series of soil nutrient concentrations, it is impossible to estimate the nutrient conditions experienced by seedlings and resprouts. Point-in-time estimates of soil nutrient concentrations may bear liitle relation to the long-term performance of the vegetation (Chapman *et al.*, 1989a).

The effect of fuel load and fire temperature on nutrient concentrations in the ash differed between stands. The nutrient content of the ash deposited after fire at the degenerate stand at Aylesbeare was not significantly different from that of the litter in the control plots. Fires at this stand were very cool and did not differ between fuel load treatments. At the mature stands, nutrient concentrations tended to be higher after high fuel load fires than after low fuel load fires, but the opposite seemed to be true for potassium and calcium at the Arne degenerate stand. The fuel loads and temperatures of the two treatments were similar at the two stands (Chapter Three), so the different responses were not related to either fuel load or temperature. High fuel load and hence high temperature fires may have caused more loss of nutrients in smoke than in low fuel load fires, therefore the nutrient content of the ash would be lower. However, a higher fuel load of vegetation contains a larger 'pool' of nutrients for deposition in the ash. The balance between these two mechanisms may have been different at the two stands, although the reasons for this are obscure.

4.4.3. Conclusions

There was no effect of burning on the seed banks of ericaceous species in the litter and soil. Therefore there is a large source of propagules for regeneration from seed after burning. The seed bank of *Erica tetralix* was depleted by the 1995 fires at the Aylesbeare mature stand, but not by the 1994 fires at the same stand. This species was dominant in the seed bank of the plots burnt in 1995, so the removal of some of the seed bank by fire would not be expected to have a significant effect on seedling densities after fire.

There was no immediate effect of burning on soil nutrient concentrations in the humic layer, but this might be expected to rise and then fall as nutrients are leached downwards from the ash. However, the time-scale for this process is not known. The concentrations of phosphorus, potassium and calcium in ash were greatest in the high fuel load fires at the Arne mature stand. This treatment at this stand produced the highest temperatures in the experiment. The more intense fires in this treatment ignited a high proportion of the vegetation (Chapter Three), which seems to be reflected in the nutrients deposited in the ash. The fires at the Aylesbeare degenerate stand burnt at very low temperatures which were not significantly different between fuel load treatments (Chapter Three). The lack of a significant difference in the concentrations of any of the nutrients studied suggests that the vegetation did not undergo complete combustion.

This study does not provide a complete picture of the nutrient fluxes following burning. The fate of nutrients in the months after fire was not investigated, yet the nutrient status at critical times such as peaks in germination and throughout the growing season is likely to have the most impact on regeneration and is worthy of further study.

CHAPTER FIVE

Vegetative regeneration after burning

5.1. Introduction

It is well-established that *Calluna* resprouts from stem bases after burning, and that this ability declines with age (e.g. Elliot, 1953; Gimingham, 1960; Kayll and Gimingham, 1965; Miller and Miles, 1970, Mohamed and Gimingham, 1970). Fire temperature and its duration affect regeneration buds (Hobbs and Gimingham, 1987), so the age of the stand that is burnt as well as the temperature at which it burns may interact to determine the post-fire regeneration (Kayll and Gimingham, 1965; Hobbs and Gimingham, 1984b, Hobbs and Gimingham, 1987).

The capacity to resprout after fire is thought to decline with age due to secondary thickening of the resprouting buds (Mohamed and Gimingham, 1970). Furthermore, degenerate stands of vegetation have a lower density of stem bases ('resprouting centres') due to self-thinning as the stand ages (Miller and Miles, 1970). These are gradual processes, and the age at which heather fails to resprout after burning varies. In Scotland, Kayll and Gimingham (1965) observed a rapid decline in resprouting from the age of 15 years but Grant (1968) noticed satisfactory regeneration from stands up to 20 - 25 years of age. Miller and Miles (1970) and Hobbs and Gimingham (1984b) found a steady decrease in the rate of regeneration with pre-burn age and no evidence of a steep decline. Hobbs and Gimingham (1984b) observed no vegetative regrowth of either *Calluna* or *Erica cinerea* when plants had reached the degenerate phase.

Secondary succession after fire depends on the differential responses of the heathland species to fire temperature and intensity (Hobbs and Gimingham, 1987). Hobbs and Legg (1984) and Hobbs and Gimingham (1984b) proposed that most successional trajectories following management burning are determined by the 'Initial Floristic Composition' (Egler, 1954, in Connell and Slatyer, 1977). The species in the pre-burn vegetation re-establish after fire from stem bases or from the seed bank. The succession involves changes in relative abundances of the species and depends largely on which species regenerate first (Hobbs and Legg, 1984). The persistence of bare ground after burning degenerate heath may allow the invasion of undesirable non-heathland species (Miller and Miles, 1970). Succession in such stands may be more complex and depend less on initial floristic composition and more on 'relay floristics' (Clements, 1916, in Connell and Slatyer, 1977) whereby other species establish in a series of replacements (Gimingham, Hobbs and Mallik, 1981; Hobbs and Gimingham, 1987). On heathlands, these species may be bracken *Pteridium aquilinum* (Hobbs, Mallik and Gimingham, 1984; Marrs, 1986; Hobbs and Gimingham, 1987) or tree species, particularly birch *Betula* spp. and pine *Pinus* spp. (Khoon and Gimingham, 1984; Gimingham, Hobbs and Mallik, 1981). Relay floristics are also typical of the succession after severe fires, when regeneration centres and propagules are destroyed (Hobbs and Legg, 1984).

The position of the regeneration buds on plant structures influence the ability of heathland species to regenerate after fire (Gimingham, Hobbs and Mallik, 1981; Reader *et al.* 1983). *Calluna* and *Erica cinerea* have regeneration buds just below or on the ground surface (chamaephytic). *Erica tetralix* resprouts from rhizome-like parts of stems below ground (Mallik and Gimingham, 1985) and so may be better protected from high temperatures. Grasses are hemicryptophytes and regrow from meristems protected by leaf sheath material (Hobbs and Gimingham, 1984b).

In the post-burn phase of vegetative regeneration (Chapman and Webb, 1978), growth can be rapid, promoted by nutrients in the deposited ash as well as food reserves in the root stocks (Chapman, Hibble and Rafarel, 1975a). Therefore net primary production is high. Net primary production is defined as the addition of plant tissue and reserve substances during a known time interval (Newbould, 1967). Estimation of net primary production involves not only the change in dry weight of vegetation per unit area over the time interval, but also the amount removed by herbivory and the biomass of litter produced. Production depends on climate, soil nutrients and moisture (Gimingham, Chapman and Webb, 1979; Miller, 1979; Diemont and Voshaar, 1994). Measurements of primary production have been made on several *Calluna*-dominated communities in the UK, including southern lowland heathland

(Chapman *et al.*, 1975 a and b); heathland in north-east Scotland (Miller, 1979), moorland (Bellamy and Holland 1966), and blanket bog (Forrest and Smith, 1975). Tyler *et al.* (1973) studied production by *Calluna* and *Erica tetralix* - dominated communities in Sweden and Diemont and Voshaar (1994) investigated biomass increment after turf-cutting and burning on both dry and humid heathland in the Netherlands.

Succession following management burning has been investigated chiefly in Scotland (e.g. Gimingham, Hobbs and Mallik, 1981; Hobbs and Legg, 1984; Hobbs and Gimingham, 1984b), where species composition, soil nutrient status and climate are different to the southern lowland heaths (Chapman and Clarke, 1980). There has been no detailed work on the succession after management fires on southern heaths with respect to changes in relative abundances and flowering vigour of the component species. The aim of this chapter is to elucidate the effects of both fire temperature and pre-burn age of the stand on immediate post-fire growth and species succession. The species composition by frequency and biomass is presented and the performance of the ericaceous species with respect to flowering and above-ground productivity is described.

5.2. Methods

5.2.1. Burning

Experiment 1. 1994 Fires

Mature and degnerate stands of vegetation were selected at two sites: Arne in Dorset and Aylesbeare in Devon (Chapter Two). Twelve plots of 5 x 5 m were laid out in a strip at each stand separated from one another by 3m to minimise ash drift. A randomised block design was used, with four replicates of two treatments plus unburnt controls at each stand. The treatments were to burn high and low fuel loads of vegetation. Burning was carried out in March 1994. The methods of vegetation manipulation and burning are described in Chapter Three. Temperatures were recorded with pyrometers consisting of temperature sensitive paints in strips on tiles.

Experiment 2. 1995 Fires

Only the Aylesbeare mature stand was used for the second experiment in March 1995. A strip of twelve plots of 3m x 2m was set up adjacent to the plots burnt in 1994. A randomised block design of two treatments plus unburnt controls was employed. Using a knapsack sprayer, 0.75 l of paraffin was evenly distributed across each of the four high fuel load treatment plots. The low fuel load treatment was to burn the existing vegetation (Chapter Three). Two methods of temperature recording were used: pyrometers as described above and thermocouples attached to a data logger.

5.2.2. Resprout Frequency

Resprout frequency of vegetatively-regenerating ericaceous shrubs in the eight burnt plots at each stand was assessed in July each year. The plots burnt in 1994 were monitored for three years, starting in July 1994. Three 1 m^2 quadrats, each divided into 100 squares, were placed randomly in each plot, avoiding the outermost metre to minimise edge effects. The number of squares in which each species rooted was counted. The frequencies of grasses, sedges, bracken and seedlings of pine and birch were also noted. The plots burnt in 1995 were monitored for two years, using just two quadrats due to the smaller size of the experimental plots.

5.2.3. Biomass

Biomass following regrowth after the 1994 fires at the mature stands was estimated by harvesting all vegetation from the eight burnt plots towards the end of each growing season (September 1994, 1995 and 1996). Two random 10cm x 1m quadrats per plot were used to encompass heterogeneity (demography quadrats and soil samples were avoided). The plots burnt at Aylesbeare in 1995 were sampled in the same way in 1995 and 1996. Vegetation was harvested from the degenerate stands (burnt in 1994) in 1996 only. Regeneration was evenly distributed at the Aylesbeare degenerate stand, so quadrats were positioned randomly. At the Arne degenerate stand, regeneration was extremely patchy, with only two or three resprouting bushes in some plots. At this stand, the area covered by each species in each plot was assessed by measuring individual bushes. Samples of 0.1 m^2 of each species were taken and the biomass of each species per 25m^2 plot was calculated. Calculation of biomass per m^2 was not performed, because this implied 100% cover and gave no indication of the relative abundances of the different species.

All samples were separated into species. The ericaceous shrubs and *Ulex* spp. were divided into unburnt stems and green material (regrowth). The unburnt stems were used in the estimation of fire intensity (Chapter Three). Ericaceous species were divided into flowering and non-flowering shoots and the number of each counted. If there were more than 100 shoots, a sub-sample of 100 was taken, and the total number of shoots estimated by dry weight. The vegetation samples were dried to constant weight in an oven at 60^{0}C.

5.2.4. Shoot Heights and Flowering

A sub-sample of 20 shoots was taken randomly from each of the ericaceous biomass samples. Hence from each plot, the heights of 40 non-flowering and 40 flowering shoots of each species were measured. If there were less than 40 shoots present in each sample, all the shoots were measured. Shoot height was measured from the base of the shoot where it had been cut at the ground surface to the tip of the leading shoot. The number of infloresences per flowering shoot and the number of flowers per infloresence were counted.

5.2.5. Rabbit activity

The activity of rabbits at each stand was assessed in September 1996 by counting the number of pellets in 10 randomly-positioned 20 x 20cm quadrats in each burnt plot. The mean for each plot was calculated and then a mean for each stand. The two burning experiments at the Aylesbeare mature stand were treated as two separate stands for this analysis.

5.2.6. Data Analysis

Trends in resprout frequency and biomass over time were distinguished using repeated measures ANOVA. ANOVA assumes that samples are independent, so repeated measurements on the same plot tend to violate this assumption, producing inflated F-values. The repeated measures procedure in SAS (SAS Institute Inc., 1989) can test this assumption by testing the variance - covariance matrix of the data for circularity. If the matrix does not exhibit circularity, adjustments to the F-values should be made. SAS calculates two adjustments, both of which are based on 'Box's ε' . Box's ε is a measure of the departure of the matrix from circularity and is in the range of 0 - 1. The Greenhouse Geisser adjustment tends to under-estimate ε, especially when the value of ε approaches zero and when sample sizes are small. For this reason, the Huynh-Feldt adjustment was used. This adjustment is less conservative and values can be greater than one. When this is the case, a value of one is used and F values are not adjusted. Unadjusted F-values were used in the analyses of the 1995 fires, because there were only two sampling periods (1995 and 1996). A sphericity test is not required when there are only two levels of the repeated factor (SAS, 1989).

Resprout frequency data for all species and percentage bare ground were arcsine transformed before ANOVA. *Calluna* occurred at similar percentage cover in the pre-burn vegetation in the mature and degenerate stands at both sites, so the resprouting frequency of this species and the percentage bare ground were compared between stands and fuel load treatments using nested repeated measures ANOVA. The other species at Aylesbeare were tested for fuel load effects on resprout frequency within stand.

The regrowth biomass of each species per m^2 and the proportion of the total biomass represented by each species was calculated from the dry weights of the vegetation samples. The biomass and number of flowering and non-flowering shoots of the ericaceous species and their relative proportions were also calculated. These variables were tested for normality and homogeneity of variances and were subjected to log or arcsine transformation if necessary. Repeated measures ANOVA was employed to test for effects of fuel load in the three growing seasons after the 1994 fires and in the two growing seasons after the 1995 fires at Aylesbeare. The 1996 biomass variables at the degenerate stands was tested for treatment effects using ANOVA.

Rabbit activity, as indicated by the density of pellets, was analysed using one-way ANOVA followed by calculation of the least significant difference (LSD) at an alpha level of 0.05 using Bonferroni's adjustment (Maxwell and Delany, 1990).

5.3. Results

5.3.1. Burning

Experiment 1. 1994 Fires

The results of burning high and low fuel loads at mature and degenerate heath at both sites are described in Chapter Three (Table 3.5). Fires in the high fuel load treatments were significantly hotter and more intense than the fires in the low fuel load treatments. The Aylesbeare degenerate stand was the exception, where all the fires were comparatively cool. Above-ground temperatures were higher than the temperatures on the litter surface, with maxima of 400 - 500°C in high fuel load fires. Litter surface temperatures were very variable. The highest mean litter surface temperature was 163°C, recorded in high fuel load fires at the Arne mature stand.

Experiment 2: 1995 Fires

There was no significant difference in mean temperature between the two burning treatments. Fire temperatures recorded by pyrometers and thermocouples are shown in Table 3.10 in Chapter Three. Pyrometers recorded mean litter surface temperatures of 200 - 300°C and above -ground temperatures of about 450°C. Thermocouples in the canopy recorded mean temperatures of about 600°C.

5.3.2. Resprout Frequency

Experiment 1. 1994 Fires

Arne

There were no significant differences between fuel load treatments at any stand in any year, therefore Table 5.1 presents the data as the means of both treatments at each stand. At the Arne mature stand, *Calluna* resprouted in over 50% of the squares in the first growing season after burning, compared with only 3% at the degenerate stand. Plate 5.1 illustrates the high percentage of bare ground in one of the plots at the degenerate stand three growing seasons after burning. Both the resprout frequency of *Calluna* and the percentage of bare ground were significantly different between stands and changed significantly at both stands over the three growing seasons following burning (Tables 5.2 and 5.3). There was no evidence of invasion by pine, birch or bracken. Pine and bracken were present in the pre-burn community at the Arne mature stand but remained at low frequency throughout the three years of post-burn monitoring. All the species observed in the regenerating vegetation were present in the vegetation before burning. However, species that were not represented in the pre-burn community were noted after burning at the degenerate stand at Arne. None of these occurred in more than three plots and were not always within quadrats, so were not analysed statistically. These species were: *Betula pendula* (1 plot in 1994, 3 plots in 1995 and 1996); *Aira praecox* (1 plot in 1994, 3 plots in 1995 and 1996); *Epilobium tetragonum* (3 plots in 1996), *Poa annua* (1 plot in 1996), *Quercus* sp. (1 plot in 1995 and 1996) and *Rumex acetosella* (1 plot, all years).

Table 5.1. Resprout frequency at all stands burnt in 1994. Values are means ± 1 SE. The two fuel load treatments were pooled (n = 8).
* *Ulex* represents *U. minor* at Arne and *U. gallii* at Aylesbeare

	Arne Mature			**Arne Degenerate**			**Aylesbeare Mature**			**Aylesbeare Degenerate**		
Species	**1994**	**1995**	**1996**	**1994**	**1995**	**1996**	**1994**	**1995**	**1996**	**1994**	**1995**	**1996**
Calluna	53.68 ± 5.84	65.28 ± 3.83	71.50 ± 4.90	3.03 ± 1.25	5.18 ± 2.27	14.33 ± 5.16	13.13 ± 3.46	13.54 ± 3.21	22.50 ± 3.69	0.62 ± 0.20	0.17 ± 0.11	4.25 ± 0.75
E. cinerea	0.04 ± 0.03	0.25 ± 0.13	1.21 ± 0.44	0.04 ± 0.03	0.53 ± 0.27	6.14 ± 2.84	4.38 ± 2.26	11.95 ± 3.48	16.92 ± 5.76	16.71 ± 4.10	17.83 ± 4.91	26.34 ± 4.55
E. tetralix				2.97 ± 2.68	4.28 ± 3.70	7.21 ± 6.21	28.96 ± 7.25	38.18 ± 8.57	50.54 ± 11.88	0.33 ± 0.29	0.29 ± 0.29	0.08 ± 0.08
Ulex *	0.58 ± 0.32	0.93 ± 0.32	0.50 ± 0.24	0.06 ± 0.04	0.19 ± 0.08	0.69 ± 0.22	34.33 ± 4.20	32.21 ± 4.54	29.46 ± 5.41	16.25 ± 1.95	21.79 ± 3.81	28.80 ± 4.07
Agrostis curtisii							35.71 ± 7.15	44.29 ± 7.96	56.79 ± 9.46	5.33 ± 1.35	17.38 ± 2.96	35.34 ± 4.69
Molinia caerulea	0.13 ± 0.13	0.01 ± 0.01	0.08 ± 0.08				22.92 ± 8.45	21.08 ± 8.74	29.46 ± 10.17	12.37 ± 6.18	17.88 ± 6.92	21.50 ± 7.82
Carex pilulifera							2.33 ± 1.41	1.04 ± 0.27	1.04 ± 0.54	0.08 ± 0.05	0.79 ± 0.36	0.50 ± 0.24
Pinus sylvestris	0.14 ± 0.06	0.04 ± 0.02	0.00 ± 0.00									
Pteridium aquilinum	1.38 ± 0.46	1.22 ± 0.38	1.44 ± 0.36							0.00 ± 0.00	0.13 ± 0.13	0.21 ± 0.21
Betula sp.				0.01 ± 0.01	0.04 ± 0.02	0.08 ± 0.05						
Polygala serpyllifolia							4.17 ± 1.12	0.58 ± 0.34	0.96 ± 0.41			
% Bare ground	65.51 ± 9.26	54.07 ± 5.81	37.15 ± 4.39	97.93 ± 5.11	91.87 ± 5.35	81.72 ± 7.71	45.76 ± 5.21	12.58 ± 2.00	11.46 ± 1.77	84.17 ± 8.67	64.34 ± 7.86	40.83 ± 5.99

Table 5.2. F-values generated by nested ANOVA on resprout frequency of *Calluna* and percentage bare ground at Arne in each year. The mean square of Block (stand) was the denominator used to calculate the F value of Stand. *** = P < 0.001, ** = 0.001 < P < 0.01, * = 0.01 < P < 0.05. NS = not significant.

Source	df	*Calluna*			Bare ground		
		1994	1995	1996	1994	1995	1996
Stand	1	44.33 **	81.40 ***	37.50 **	25.53 **	38.01 ***	12.62 *
Fuel Load	1	0.79 NS	1.32 NS	1.90 NS	0.32 NS	0.15 NS	0.26 NS
Block (stand)	6	6.97 *	3.82 NS	2.21 NS	2.71 NS	1.17 NS	1.11 NS
Stand x Fuel Load	1	1.25 NS	2.79 NS	0.42 NS	0.04 NS	0.34 NS	0.02 NS

Table 5.3. F-values generated by nested repeated measures ANOVA on resprout frequency of *Calluna* and percentage bare ground at Arne. Mean square of Block (Stand) was the denominator used to test Stand and Time x Block (Stand) was used to test Time x Stand

	df	Source	*Calluna*	Bare ground
Between plot factors	1	Stand	55.63 ***	25.41 **
	1	Fuel Load	1.59 NS	0.25 NS
	6	Block (Stand)	3.74 NS	1.48 NS
	1	Stand x Fuel Load	1.24 NS	0.04 NS
Within plot factors	2	Time	51.69 **	30.49 ***
	2	Time x Stand	1.51 NS	11.17 **
	2	Time x Fuel Load	1.52 NS	0.08 NS
	12	Time x Block (Stand)	1.79 NS	1.16 NS
	2	Time x Stand x Fuel Load	0.29 NS	1.13 NS

Aylesbeare

At Aylesbeare, the *Calluna* resprout frequency and the percentage of bare ground were also significantly different between stands and changed significantly over time (Tables 5.4 and 5.5). Plate 5.2. illustrates the high percentage of bare ground and unburnt stems in one of the plots at the degenerate stand three growing seasons after burning. *Calluna* resprout frequency at the degenerate stand remained at less than 5% throughout the recording period (Table 5.1), despite being co-dominant in the pre-burn community (Chapter Two). There were no significant differences between treatments for any species at either stand at any time (Table 5.4).

Plate 5.1. The Aylesbeare degenerate stand in 1996

Plate 5.2. The Arne degenerate stand in 1996

Table 5.4. F-values generated by nested ANOVA on resprout frequency of *Calluna* and percentage bare ground at Aylesbeare in each year. The mean square of Block (stand) was the denominator used to calculate the F value of Stand.

Source	df	*Calluna* 1994	*Calluna* 1995	*Calluna* 1996	Bare ground 1994	Bare ground 1995	Bare ground 1996
Stand	1	14.62 **	93.55 ***	36.04 **	416.44 ***	104.10 ***	34.12 **
Fuel Load	1	0.49 NS	0.71 NS	5.88 NS	0.91 NS	0.12 NS	0.19 NS
Block (stand)	6	7.65 *	0.31 NS	1.23 NS	1.61 NS	0.62 NS	2.29 NS
Stand x Fuel Load	1	0.05 NS	0.71 NS	0.64 NS	0.91 NS	0.03 NS	3.11 NS

Table 5.5. F values generated by nested repeated measures ANOVA on resprout frequency of *Calluna* and percentage bare ground at Aylesbeare. Mean square of Block (Stand) was the denominator used to test Stand and Time x Block (Stand) was used to test Time x Stand

	df	Source	*Calluna*	Bare ground
Between plot factors	1	Stand	41.32 ***	31.28 **
	1	Fuel Load	1.33 NS	0.32 NS
	6	Block (Stand)	1.43 NS	0.62 NS
	1	Stand x Fuel Load	0.61 NS	0.06 NS
Within plot factors	2	Time	30.80 ***	71.42 ***
	2	Time x Stand	0.71 NS	1.26 NS
	2	Time x Fuel Load	4.11 *	0.14 NS
	12	Time x Block (Stand)	1.37 NS	2.34 NS
	2	Time x Stand x Fuel Load	0.61 NS	2.34 NS

At the mature stand, only *Calluna*, *Erica tetralix* and *Molinia caerulea* varied significantly over time (Tables 5.5 and 5.6). The other common species, *Ulex gallii*, *Erica cinerea* and *Agrostis curtisii* did not change significantly in resprout frequency throughout the recording period. *Erica tetralix*, *Agrostis curtisii* and *Ulex gallii* were co-dominant in the post-burn vegetation. *Calluna* was comparatively infrequent.

At the degenerate stand, *Erica tetralix*, which occurred at very low frequency (Table 5.1) was the only species not to increase over time (Table 5.6). *Erica cinerea* and *Ulex gallii* were common throughout the recording period and *Agrostis curtisii* increased from a very low frequency in the first growing season after burning to become the most frequent species by 1996. *Molinia caerulea* also achieved a high mean frequency, but did not occur in all plots. There was no evidence of invasion by non-heathland species at any of the stands.

Table 5.6. F-values generated by repeated measures ANOVA on resprout frequency of species at Aylesbeare

	df	Source	*Erica cinerea*	*Erica tetralix*	*Ulex gallii*	*Agrostis curtisii*	*Molinia caerulea*
Aylesbeare Mature							
Between plot factors	1	Fuel Load	0.09 NS	0.00 NS	2.74 NS	0.09 NS	0.10 NS
	3	Block	0.86 NS	0.35 NS	0.77 NS	0.29 NS	1.33 NS
Within plot factors	2	Time	3.40 NS	18.37 **	3.28 NS	15.03 **	10.06 *
	2	Time x Fuel Load	0.03 NS	0.18 NS	0.45 NS	0.67 NS	0.48 NS
	6	Time x Block	1.64 NS	0.28 NS	2.77 NS	0.62 NS	0.99 NS
Aylesbeare Degenerate							
Between plot factors	1	Fuel Load	0.24 NS	1.43 NS	0.19 NS	1.17 NS	0.92 NS
	3	Block	1.66 NS	1.00 NS	1.19 NS	2.97 NS	5.93 NS
Within plot factors	2	Time	15.18 **	1.78 NS	55.89 ***	111.45 ***	24.64 **
	2	Time x Fuel Load	4.76 NS	1.78 NS	3.51 NS	0.14 NS	2.33 NS
	6	Time x Block	0.13 NS	1.00 NS	28.10 ***	0.87 NS	4.42 NS

Experiment Two: 1995 Fires

The frequency of resprouts of *Erica cinerea* was significantly less after burning plots with added paraffin than plots with no added paraffin (Tables 5.7 and 5.8). None of the other species was affected. *Carex pilulifera* and *Polygala serpyllifolia* were very infrequent (only one or two plots), and thus were not analysed. Repeated measures ANOVA (Table 5.8) shows that the resprout frequencies of all species except the grasses were significantly different between the two sampling dates. However, only *Erica tetralix* increased over time; the other species were less frequent in 1996 than they were in 1995.

Table 5.7. F-values generated by ANOVA showing effect of burning with or without paraffin on resprout frequencies at the Aylesbeare mature stand (1995 Fires). *Agrostis = Agrostis curtisii, Molinia = Molinia caerulea, Carex = Carex pilulifera, Polygala = Polygala serpyllifolia.* N/A = not analysed (see text)

	1995			1996		
Species	**-paraffin**	**+paraffin**	**F**	**-paraffin**	**+paraffin**	**F**
Calluna	63.87 ± 1.33	52.80 ± 12.00	1.09 NS	54.50 ± 2.52	49.50 ±11.20	0.20 NS
E. cinerea	40.62 ± 4.56	13.38 ± 2.75	18.67 **	31.38 ± 5.79	7.25± 2.59	10.38 *
E. tetralix	48.30 ± 13.00	44.60 ± 14.60	0.50 NS	55.90 ± 12.60	53.00 ± 14.30	0.16 NS
Ulex gallii	21.50 ± 0.82	24.00 ± 5.84	0.20 NS	15.50 ± 0.84	14.63 ± 5.95	0.02 NS
Agrostis	42.80 ± 13.50	41.90 ± 12.60	0.05 NS	47.50 ± 15.70	49.50 ± 14.10	0.05 NS
Molinia	19.60 ± 13.30	35.10 ± 12.70	0.81 NS	15.10 ± 10.70	34.20 ± 11.40	1.75 NS
Carex	0.00 ± 0.00	0.25 ± 0.14	N/A	0.25 ± 0.25	0.00 ± 0.0	N/A
Polygala	0.13 ± 0.13	0.88 ± 0.88	N/A	2.13 ± 0.59	2.00 ± 0.98	N/A
% Bare ground	70.62 ± 3.87	70.00 ± 4.79	0.01 NS	15.62 ± 4.13	19.38 ± 4.83	0.33 NS

Table 5.8. F-values generated by repeated measures ANOVA on resprout frequencies at the Aylesbeare mature stand (1995 Fires)

	Between-plot factors		Within-plot factors		
Species	**Paraffin**	**Block**	**Time**	**Time x paraffin**	**Time x Block**
Calluna	0.56 NS	1.34 NS	11.79 *	2.78 NS	0.27 NS
E. cinerea	14.09 *	0.43 NS	54.36 **	2.25 NS	0.30 NS
E. tetralix	0.28 NS	18.71 *	36.04 **	0.08 NS	4.70 NS
Ulex gallii	0.02 NS	1.05 NS	117.28 **	5.65 NS	0.83 NS
Agrostis	0.01 NS	17.53 *	4.62 NS	0.25 NS	0.37 NS
Molinia	1.21 NS	1.31 NS	1.75 NS	0.80 NS	0.89 NS
% Bare ground	0.07 NS	1.05 NS	3173.44 ***	5.44 NS	1.59 NS

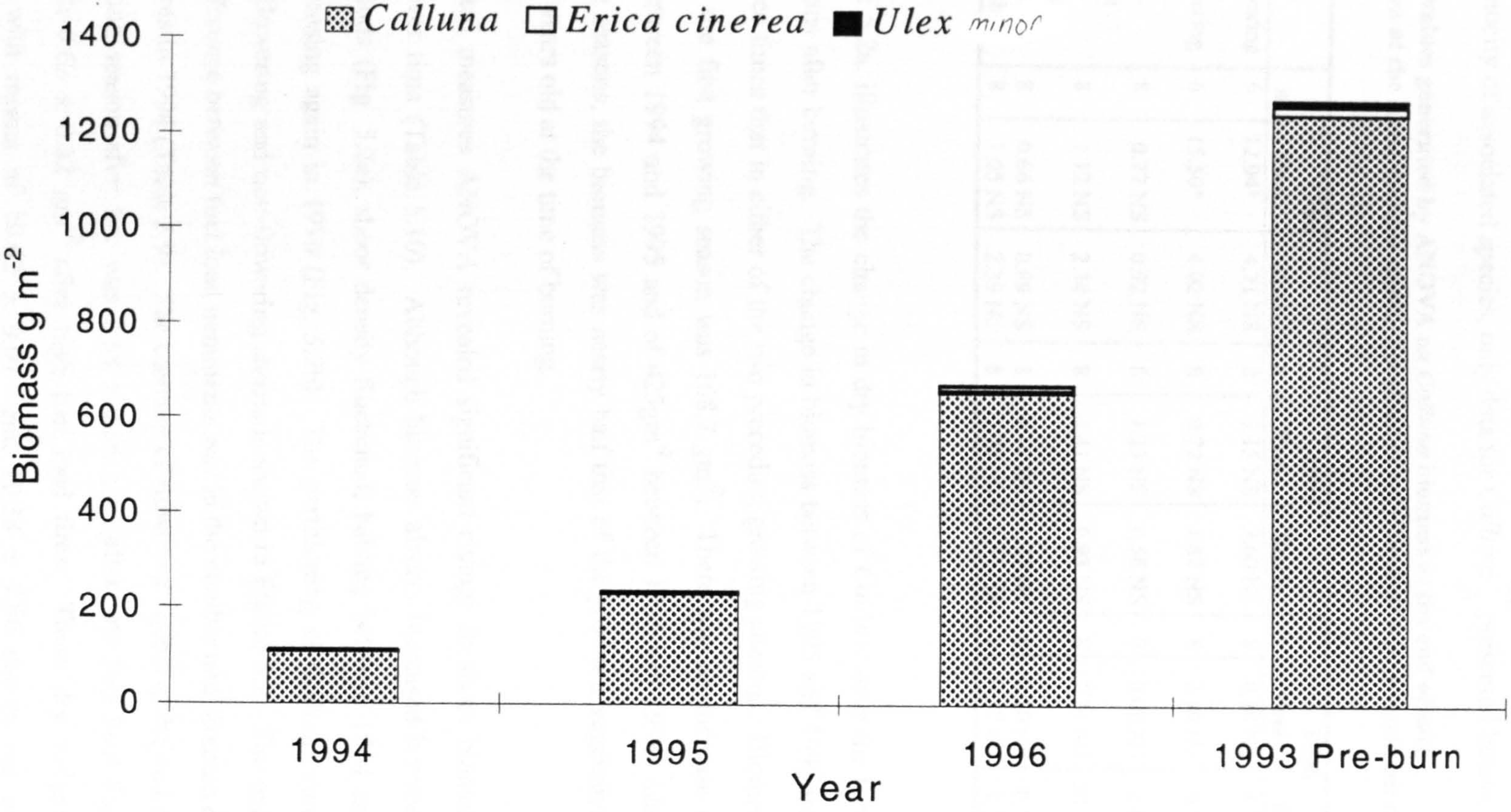
5.3.2. Biomass, Productivity and Flowering

Experiment 1: 1994 Fires

Arne mature stand

There was no difference in the total biomass of *Calluna* shoots between the two burning treatments (Table 5.9), and therefore data were pooled for graphical presentation. Figure 5.1 shows the dominance of *Calluna* in the vegetation both before and after burning. Other species were rare. *Ulex minor* occurred in only one plot in 1994 and in four plots in 1995 and 1996. *Erica cinerea* was sparsely

Fig. 5.1. Biomass composition of regenerating and pre-burn vegetation at the Arne mature stand



distributed and was only found in two plots in 1994 and 1996 and three plots in 1995. Due to the paucity of associated species, only data for *Calluna* are presented below.

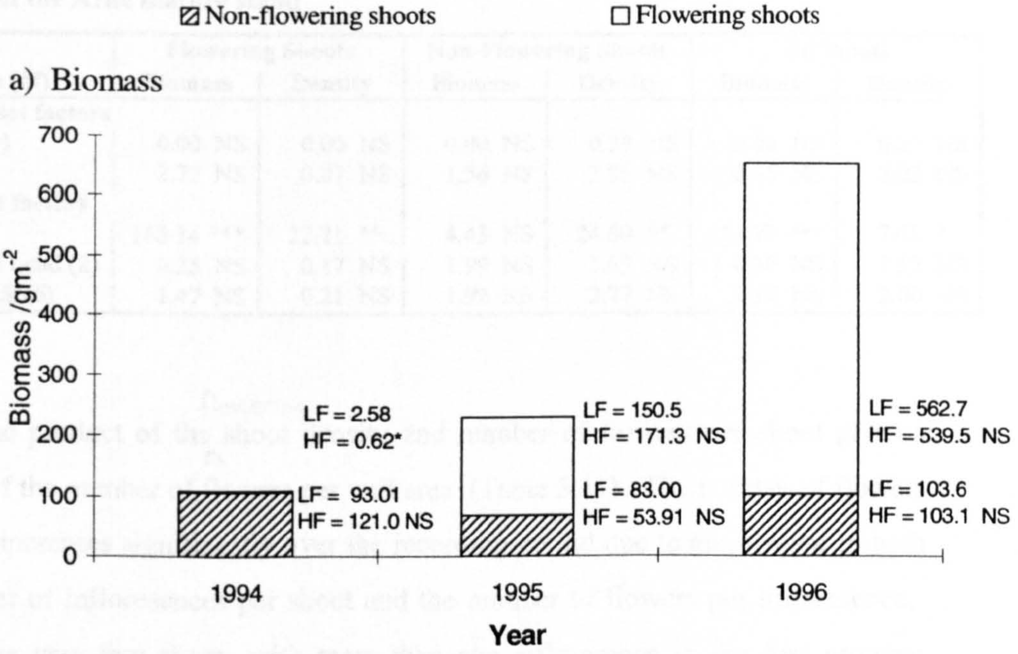
Table 5.9. F-values generated by ANOVA on *Calluna* biomass at the end of each growing season at the Arne mature stand. Fuel load df = 1; Block df = 3. n = number of plots.

	1994			1995			1996		
Variable	**n**	**Fuel**	**Block**	**n**	**Fuel**	**Block**	**n**	**Fuel**	**Block**
Biomass of flowering shoots	6	12.94*	4.71 NS	8	1.15 NS	3.60 NS	8	0.10 NS	1.75 NS
Number of flowering shoots	6	15.50*	4.02 NS	8	0.72 NS	1.82 NS	8	0.10 NS	0.09 NS
Biomass of non-flowering shoots	8	0.77 NS	0.92 NS	8	1.33 NS	0.56 NS	8	0.00 NS	8.09 NS
Number of non-flowering shoots	8	1.12 NS	2.34 NS	8	4.41 NS	0.93 NS	8	2.21 NS	24.33 *
Total shoot biomass	8	0.66 NS	0.89 NS	8	0.17 NS	1.77 NS	8	0.10 NS	0.75 NS
Total shoot number	8	1.05 NS	2.39 NS	8	3.79 NS	0.52 NS	8	0.37 NS	1.71 NS

Figure 5.2a. illustrates the change in dry biomass of *Calluna* over the three growing seasons after burning. The change in biomass between 1995 and 1996 was more than three times that in either of the two preceding growing seasons. Biomass at the end of the first growing season was 108.7 gm^{-2}. There was an increase of 120.7 gm^{-2} between 1994 and 1995 and of 425gm^{-2} between 1995 and 1996. After three growing seasons, the biomass was nearly half that of the pre-burn vegetation, which was 21 years old at the time of burning.

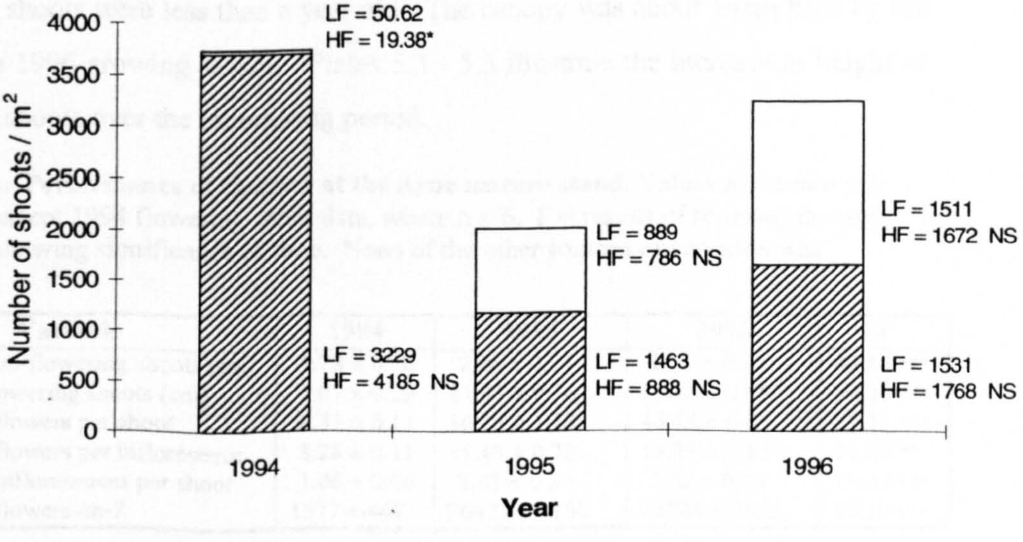
Repeated measures ANOVA revealed significant change in shoot biomass and density over time (Table 5.10). Although biomass always increased between recording periods (Fig. 5.2a), shoot density fluctuated, halving between 1994 and 1995 but increasing again in 1996 (Fig. 5.2b). The partitioning of *Calluna* shoot biomass into flowering and non-flowering shoots is shown in Figure 5.2. The only significant difference between fuel load treatments was in the number and biomass of flowering shoots in 1994 (Table 5.9). The biomass of flowering shoots at the end of the first growing season after fire was 2.58 ± 0.86 gm^{-2} after low fuel load fires compared with 0.62 ± 0.32 gm^{-2} after high fuel load fires. These dry weights corresponded with means of 50.62 ± 9.97 and 19.38 ± 7.66 shoots per m^{2}

Fig. 5.2. *Calluna* regrowth at the Arne mature stand. Bars are means of pooled treatments and annotations are treatment means (flowering shoots above, non-flowering shoots below). LF = low fuel load fires, HF = high fuel load fires, * = $0.01 < p < 0.05$, NS = not significant



a) Biomass

b) Shoot density



respectively. The contribution of flowering shoots to the overall biomass was less than 2% (1 % of shoots) in this year but increased to over 80% (50% of shoots) by the end of the 1996 growing season. The biomass and density of flowering shoots increased significantly over time (Table 5.10, Fig 5.2).

Table 5.10. F-values generated by repeated measures ANOVA of *Calluna* biomass variables at the Arne mature stand

	Flowering Shoots		**Non-Flowering Shoots**		**All shoots**	
Source (df)	**Biomass**	**Density**	**Biomass**	**Density**	**Biomass**	**Density**
Between- plot factors						
Fuel load (1)	0.00 NS	0.00 NS	0.00 NS	0.39 NS	0.00 NS	0.27 NS
Block (3)	2.72 NS	0.07 NS	1.56 NS	2.96 NS	0.35 NS	2.02 NS
Within-plot factors						
Time (2)	168.14 ***	22.21 **	4.43 NS	24.60 **	153.70 ***	7.42 *
Time x Fuel Load (2)	0.25 NS	0.17 NS	1.99 NS	1.99 NS	0.30 NS	1.57 NS
Time x Block (6)	1.47 NS	0.21 NS	1.92 NS	2.77 NS	1.16 NS	2.00 NS

The product of the flowering shoot density and number of flowers per shoot gives a measure of the number of flowers per unit area (Table 5.11). The number of flowers per shoot increases significantly over the recording period due to an increase in both the number of infloresences per shoot and the number of flowers per infloresence. There were very few shoots with more than one infloresence in the first growing season, but by 1996 the mean number per shoot was more than three (Table 5.11). Flowering shoots were taller than non-flowering shoots and the difference between them increased with time. Presumably this is because a higher proportion of the non-flowering shoots were less than a year old. The canopy was about 16cm high by the end of the 1996 growing season. Plates 5.3 - 5.5 illustrate the increase in height of flowering shoots over the monitoring period.

Table 5.11. Performance of *Calluna* at the Arne mature stand. Values are means ± 1 SE. n=8, except 1994 flowering shoot data, where n = 6. F = results of repeated measures ANOVA, showing significance of time. None of the other sources of variation was significant

Variable	**1994**	**1995**	**1996**	**F**
Height of non-flowering shoots (cm)	4.78 ± 0.16	7.26 ± 0.24	8.35 ± 0.25	43.84 ***
Height of flowering shoots (cm)	5.07 ± 0.29	11.95 ± 0.34	16.73 ± 0.65	59.86 ***
Number of flowers per shoot	8.31 ± 0.11	30.87 ± 3.33	48.59 ± 6.40	29.11 ***
Number of flowers per infloresence	8.28 ± 0.11	11.43 ± 0.73	13.89 ± 0.83	11.22 **
Number of infloresences per shoot	1.06 ± 0.06	2.63 ± 0.20	3.52 ± 0.44	29.40 ***
Number of flowers /m-2	1577 ± 407	26421 ± 4166	72528 ± 7658	55.10 ***

Plate 5.3. *Calluna* resprouts at Arne in 1994

Plate 5.4. ***Calluna*** **resprouts at Arne in 1995**

Plate 5.5 ***Calluna*** **resprouts at Arne in 1996**

Arne degenerate stand

Regeneration at this stand was patchy, with striking differences between plots, but no difference between fuel load treatments. Figure 5.3 illustrates the differences between individual plots at this stand and compares the pre-burn biomass in 1993 with the biomass three growing seasons after burning. The two graphs are on different scales due to the method used to sample biomass in the burnt plots (section 5.2.3). The biomass in all plots (except HF4, Fig. 5.3a) three growing seasons after burning was only about 10% of the pre-burn vegetation.*Calluna* was dominant in every plot before burning. *Erica tetralix* occurred at low cover in block 4 before burning (Fig. 5.3b), but was dominant in the regenerating vegetation in this block (Fig. 5.3a). *Erica cinerea* was more abundant than *Calluna* in blocks two and three after burning, but *Calluna* was more frequent in block 1 (Fig. 5.3a). *Agrostis curtisii* occurred in one control plot in the pre-burn vegetation (see Chapter Two).

The biomass of each species per plot indicates the relative abundances of the component species, but, due to the patchy distribution of these species it is not informative to calculate the density of shoots or flowers. However, the regenerating plants were growing vigorously and produced many flowers per shoot (Table 5.12).

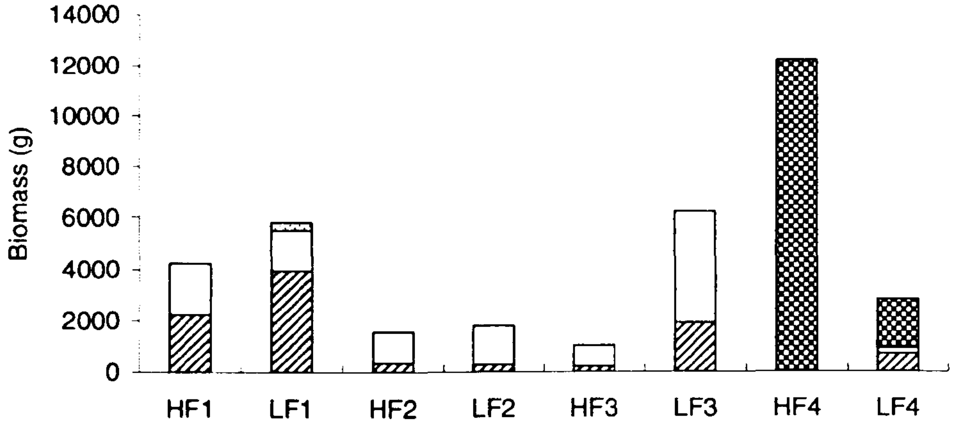
Table 5.12. Performance in 1996 of ericaceous species at the Arne degenerate stand after burning

	Calluna		*Erica cinerea*		*Erica tetralix*	
Variable	**n**	**$\bar{x} \pm$ SE**	**n**	**$\bar{x} \pm$ SE**	**n**	**$\bar{x} \pm$ SE**
Height of non-flowering shoots (cm)	6	8.99 ± 0.54	1	3.90	1	13.21
Height of flowering shoots (cm)	8	21.12 ± 1.15	7	21.47 ± 1.11	2	23.81 ± 1.76
Number of flowers per shoot	8	168.8 ± 28.9	7	79.2 ± 21.1	2	34.95 ± 9.65
Number of flowers per infloresence	8	21.21 ± 1.18	7	12.6 ± 1.36	2	9.17 ± 1.20
Number of infloresences per shoot	8	7.05 ± 0.97	7	6.29 ± 1.16	2	3.75 ± 1.20

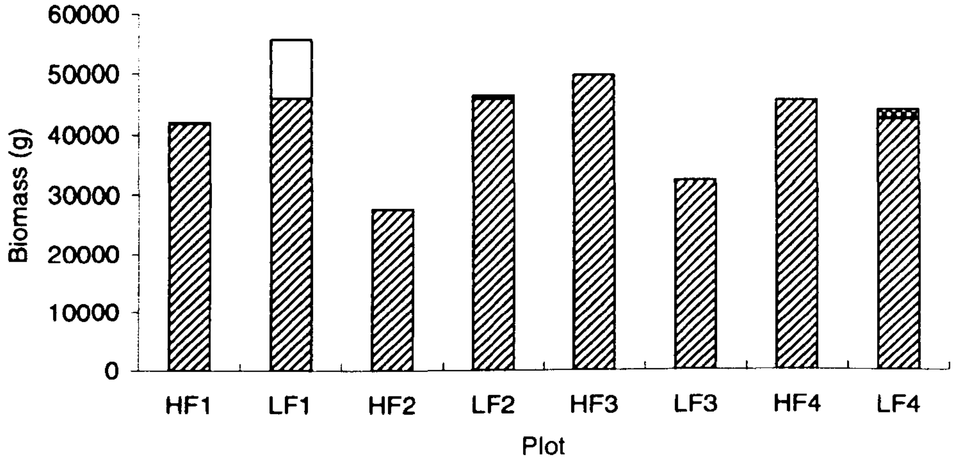
Figure 5.3. Vegetation biomass per 25m^2 plot at the Arne degenerate stand. HF = high fuel load plots, LF = low fuel load plots (blocks 1-4)

▨ *Calluna* ☐ *Erica cinerea* ▦ *Erica tetralix* ⊡ *Agrostis curtisii*

a) Regrowth in 1996



b) Pre-burn in 1993



Aylesbeare mature stand

Figure 5.4 shows the contributions of the main species to the overall biomass. *Polygala serpyllifolia* and *Carex pilulifera* were also present, but in amounts too small to record on the scale of these graphs.

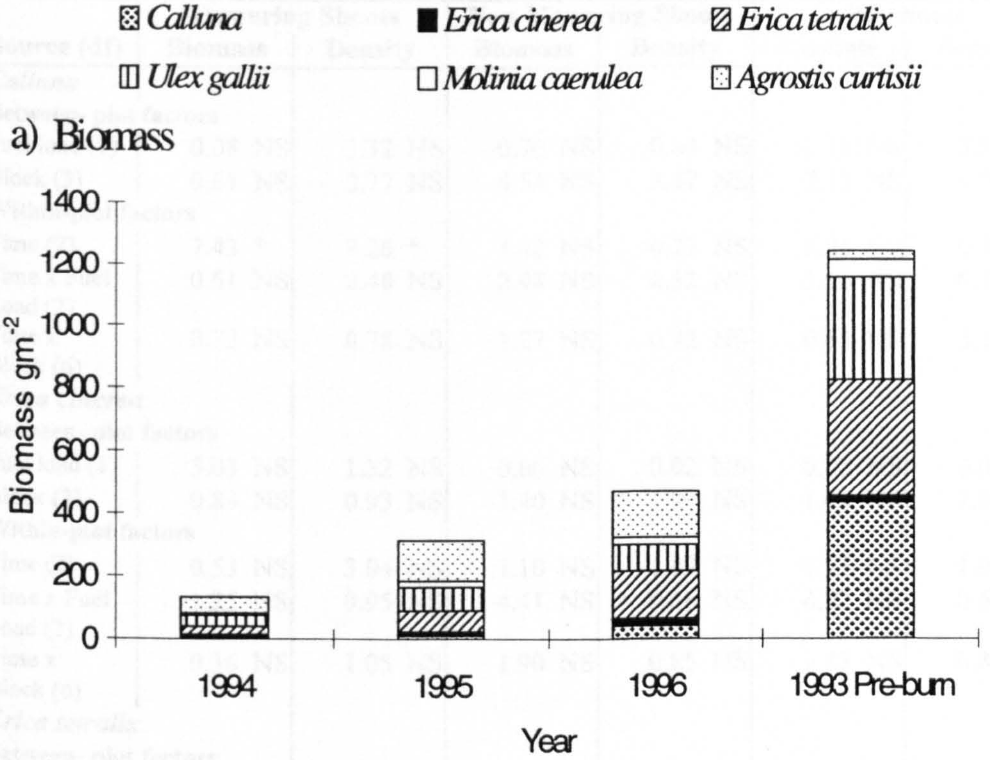
There were no significant differences between fuel load treatments in the regeneration of any species, therefore only the repeated measures ANOVAs are shown in Tables 5.13 and 5.14. Total biomass increased significantly over the recording period. The increase in biomass between each sampling period was about 150 gm^{-2} (Fig. 5.4a). The standing biomass was about 140 gm^{-2} in 1994 and 450gm^{-2} in 1996. The biomass of all species except *Erica cinerea* increased significantly over the recording period (Tables 5.13 and 5.14).

Table 5.13. F-values generated by repeated measures ANOVA on biomass of non-ericaceous species and total biomass at the Aylesbeare mature stand

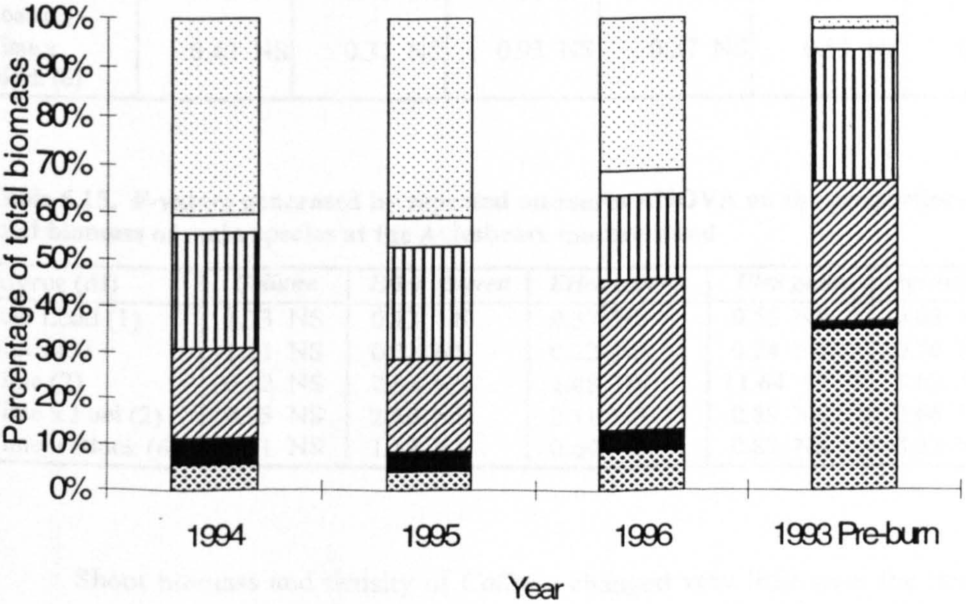
Source (df)	*Ulex gallii*	*Agrostis curtisii*	*Total biomass*
Fuel Load (1)	0.55 NS	0.63 NS	0.11 NS
Block (3)	0.74 NS	0.70 NS	9.11 NS
Time (2)	11.64 **	5.83 **	18.19 **
Time x Fuel (2)	0.89 NS	0.66 NS	0.59 NS
Time x Block (6)	0.87 NS	0.82 NS	1.07 NS

Molinia caerulea, *Carex pilulifera* and *Polygala serpyllifolia* were not analysed due to their patchy distributions in space and time. Only *Agrostis curtisii* and *Ulex gallii* varied over time in relative proportions (Table 5.15). There was little difference between the first two growing seasons, but the relative proportions of both species decreased in 1996 (Fig. 5.4b). The relative proportion of *Erica tetralix* to the overall biomass increased from about 20% in 1994 to more than 30% in 1996 and *Calluna* increased from about 5% to 8.5% in the same period, but these changes were not significant (Table 5.15).

Fig. 5.4. Biomass composition of regenerating and pre-burn vegetation at the Aylesbeare mature stand.



a) Biomass



b) Relative proportions of species

Table 5.14. F-values generated by repeated measures ANOVA on biomass variables of ericaceous species at the Aylesbeare mature stand

	Flowering Shoots		Non-Flowering Shoots		All shoots	
Source (df)	**Biomass**	**Density**	**Biomass**	**Density**	**Biomass**	**Density**
Calluna						
Between- plot factors						
Fuel load (1)	0.08 NS	3.32 NS	0.70 NS	0.64 NS	1.15 NS	0.53 NS
Block (3)	0.61 NS	2.77 NS	4.54 NS	3.47 NS	7.17 NS	3.70 NS
Within-plot factors						
Time (2)	7.43 *	9.26 *	4.42 NS	0.22 NS	5.25 *	0.49 NS
Time x Fuel Load (2)	0.61 NS	2.48 NS	2.48 NS	0.52 NS	3.66 NS	0.71 NS
Time x Block (6)	0.73 NS	0.78 NS	1.27 NS	0.72 NS	0.63 NS	0.77 NS
Erica cinerea						
Between- plot factors						
Fuel load (1)	5.03 NS	1.32 NS	0.06 NS	0.02 NS	0.03 NS	0.02 NS
Block (3)	0.83 NS	0.93 NS	1.40 NS	1.99 NS	1.42 NS	1.98 NS
Within-plot factors						
Time (2)	0.53 NS	3.04 NS	1.10 NS	1.09 NS	0.71 NS	1.02 NS
Time x Fuel Load (2)	1.25 NS	0.95 NS	4.41 NS	0.66 NS	4.22 NS	0.60 NS
Time x Block (6)	0.36 NS	1.05 NS	1.90 NS	0.85 NS	1.43 NS	0.85 NS
Erica tetralix						
Between- plot factors						
Fuel load (1)	0.86 NS	0.29 NS	0.52 NS	0.48 NS	0.67 NS	0.45 NS
Block (3)	0.40 NS	0.39 NS	0.46 NS	0.66 NS	0.43 NS	0.61 NS
Within-plot factors						
Time (2)	7.81 *	6.54 *	0.54 NS	3.25 NS	6.95 *	1.91 NS
Time x Fuel Load (2)	1.72 NS	1.05 NS	0.01 NS	0.45 NS	1.38 NS	0.29 NS
Time x Block (6)	0.42 NS	0.37 NS	0.93 NS	0.37 NS	0.57 NS	0.37 NS

Table 5.15. F-values generated by repeated measures ANOVA on the proportions of total biomass of main species at the Aylesbeare mature stand

Source (df)	***Calluna***	***Erica cinerea***	***Erica tetralix***	***Ulex gallii***	***Agrostis curtisii***
Fuel Load (1)	1.73 NS	0.13 NS	0.37 NS	0.55 NS	0.63 NS
Block (3)	1.11 NS	0.72 NS	0.22 NS	0.74 NS	0.70 NS
Time (2)	0.12 NS	2.54 NS	1.88 NS	11.64 **	5.83 **
Time x Fuel (2)	0.73 NS	2.30 NS	2.11 NS	0.89 NS	0.66 NS
Time x Block (6)	0.91 NS	1.17 NS	0.69 NS	0.87 NS	0.82 NS

Shoot biomass and density of *Calluna* changed very little over the first two growing seasons, with approximately 400 shoots m^{-2} weighing about 15 g (Figs. 5.5a

Fig. 5.5. Regrowth biomass of ericaceous species at the Aylesbeare mature stand

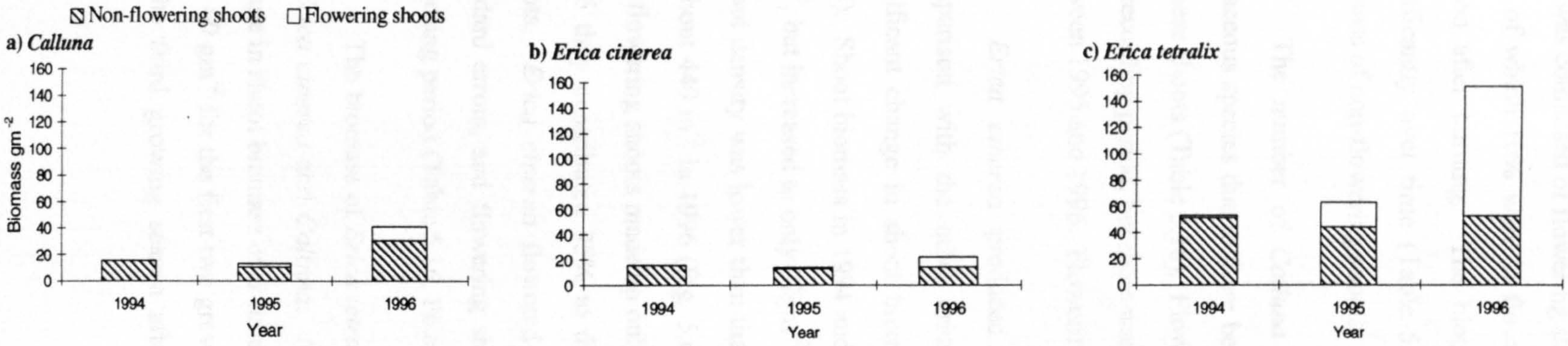
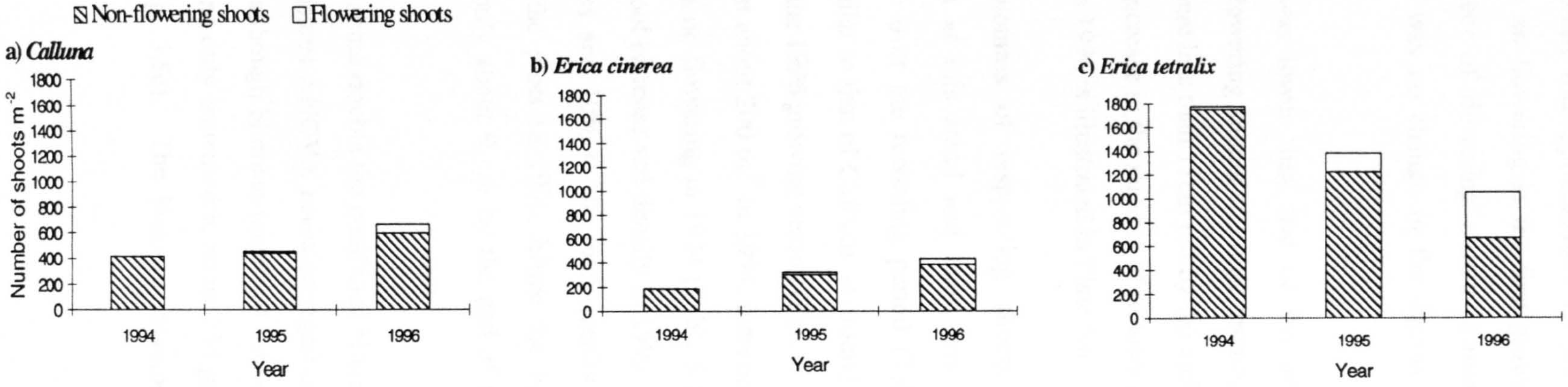


Fig. 5.6. Shoot densities of ericaceous species at the Aylesbeare mature stand



and 5.6a). Biomass increased by 25 gm^{-2} between 1995 and 1996 and about 25% of this was composed of flowering shoots. Shoot density was approximately 650 shoots m^{-2}, of which 10% were in flower. There was no flowering in the first growing season after burning. The biomass and number of flowering shoots increased significantly over time (Table 5.14) but there was no change in the density or biomass of non-flowering shoots.

The number of *Calluna* flowers m^{-2} was lower than that of the other ericaceous species due to there being very few flowering shoots and little branching of these shoots (Table 5.16). Flowering shoots were less than 11cm tall by the end of the recording period, but there was a significant increase in the number of flowers m^{-2} between 1995 and 1996. Flowering of *Calluna* in 1996 is illustrated in Plate 5.6.

Erica cinerea produced the lowest biomass of resprouting shoots in comparison with the other ericaceous species at this stand and there was no significant change in shoot biomass or density over the recording period (Table 5.14). Shoot biomass in 1994 and 1995 was similar to that of *Calluna*, at around 15 gm^{-2}, but increased to only 22gm^{-2} by the end of the 1996 growing season (Fig. 5.5b). Shoot density was lower than that of *Calluna*, at about 200 m^{-2} in 1994, increasing to about 440 m^{-2} in 1996 (Fig. 5.6b). There was no flowering in 1994 (Table 5.16) and flowering shoots made up only 5% of the shoot biomass and density in 1995. In 1996 they contributed 35% to the total biomass and 10% to the total density of shoots. *Erica cinerea* flowered in only half the plots in 1996, hence the high standard errors, and flowering shoots reached only about 9 cm by the end of the recording period (Table 5.16, Plate 5.7).

The biomass of *Erica tetralix* shoots was about double the combined biomass of *Erica cinerea* and *Calluna*. A repeated measures ANOVA revealed significant change in shoot biomass over time (Table 5.14), although biomass remained between 50 - 60 gm^{-2} for the first two growing seasons, and only increased to about 150 gm^{-2} in the third growing season after burning (Fig. 5.5c). The biomass increment

Plate 5.6. *Calluna* resprouts at the Aylesbeare mature stand in 1996

Plate 5.7. *Erica cinerea* resprouts at the Aylesbeare mature stand in 1996

between 1994 and 1995 was only 9.4 gm^{-2}, compared with 88.1 gm^{-2} between 1995 and 1996.

Table 5.16. Performance of ericaceous species at the Aylesbeare mature stand. Values are means ± 1 SE. n= number of plots. F = results of repeated measures ANOVA, showing significance of time. None of the other sources of variation was significant

	Year						
Variable		**1994**		**1995**		**1996**	**F**
Calluna	**n**		**n**		**n**		
Height of non-flowering shoots (cm)	8	2.03 ± 0.20	8	3.40 ± 0.16	8	6.17 ± 0.47	20.88 **
Height of flowering shoots (cm)	0		5	7.08 ± 0.87	8	10.81 ± 0.50	9.51 *
Number of flowers per shoot	0		5	8.53 ± 1.19	8	11.35 ± 2.45	21.31 **
Number of flowers per infloresence	0		5	8.53 ± 1.19	8	9.23 ± 2.04	2.70 NS
Number of infloresences per shoot	0		5	1.00 ± 0.00	8	1.53 ± 0.09	5.12 NS
Number of flowers m^{-2}	0		8	127 ± 65.6	8	836 ± 335	8.96 *
Erica cinerea							
Height of non-flowering shoots (cm)	7	1.92 ± 0.25	8	3.66 ± 0.47	8	4.61 ± 0.29	6.72 *
Height of flowering shoots (cm)	0		4	6.29 ± 1.21	4	9.7 ± 1.62	0.74 NS
Number of flowers per shoot	0		4	3.30 ± 0.46	4	8.76 ± 3.38	11.47**
Number of flowers per infloresence	0		4	3.30 ± 0.46	4	4.75 ± 1.20	3.48 NS
Number of infloresences per shoot	0		4	1.00 ± 0.00	4	1.58 ± 0.33	6.21 *
Number of flowers m^{-2}	0	0.0	8	69 ± 45.2	8	948 ± 812	1.26 NS
Erica tetralix							
Height of non-flowering shoots (cm)	8	4.75 ± 0.39	8	4.64 ± 0.19	8	8.87 ± 0.74	1.90 NS
Height of flowering shoots (cm)	6	7.67 ± 0.39	7	11.54 ± 0.53	7	15.75 ± 0.67	2.72 NS
Number of flowers per shoot	6	6.09 ± 1.63	7	6.95 ± 0.53	7	12.19 ± 1.66	2.09 NS
Number of flowers per infloresence	6	6.09 ± 1.63	7	6.83 ± 0.50	7	8.09 ± 0.40	0.39 NS
Number of infloresences per shoot	6	1.00 ± 0.00	7	1.02 ± 0.01	7	1.55 ± 0.11	1.48 NS
Number of flowers m^{-2}	8	141 ± 47.7	8	1159 ± 315	8	5247 ± 1813	8.23 *

Shoot density tended to decrease over time (Fig. 5.6c), but this decline was not significant (Table 5.14). The contribution of flowering shoots to total biomass and number of shoots increased significantly (Table 5.14, Figs 5.5c and 5.6c). The

Plate 5.8. *Erica tetralix* regeneration at the Aylesbeare mature stand in 1996

proportion of the biomass composed of flowering shoots increased from 2% (1% by number) in 1994 to over 70% (35% by number) in 1996. There was no change in the biomass or density of non-flowering shoots (Table 5.14). Plate 5.8 illustrates flowering of *Erica tetralix.*

Erica tetralix was the only ericaceous species to flower in the first growing season after burning and flowered prolifically in 1995 and 1996 (Table 5.16). Flowering shoots reached more than 15cm tall by the end of the monitoring period. Branching was not extensive, but the pattern of branching of both *Erica* species is different from that of *Calluna* (Gimingham, 1972), so the genera cannot be compared.

Aylesbeare degenerate stand

In 1996, three growing seasons after burning, the regrowth biomass was less than 25% of the pre-burn biomass (Fig. 5.7a). *Erica cinerea*, *Ulex gallii* and *Agrostis curtisii* were co-dominant in the regenerating vegetation. *Calluna* was extremely sparse (0.73 ± 0.40 gm^{-2}) and did not flower. *Calluna* was found in six plots and the mean shoot height was only 6.63 ± 1.07 cm The grasses *Agrostis curtisii* and *Molinia caerulea* were uncommon before burning, but together constituted 45% of the biomass in 1996 (Fig. 5.7b).

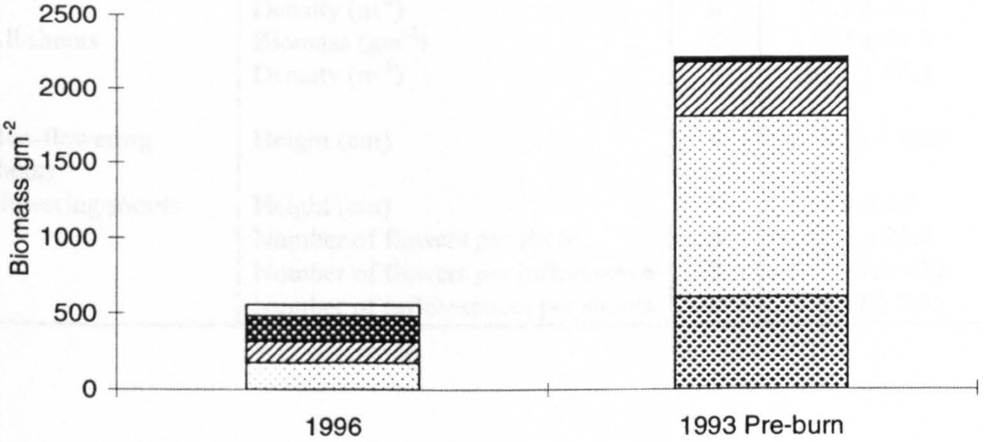
The performance of *Erica cinerea* is shown in Table 5.17. Flowering shoots constituted over 98% of the biomass (85% of shoots). Non-flowering shoots were found in only four plots and were only about 7cm tall.

Figure 5.7. Biomass composition of regenerating vegetation and pre-burn vegetation at the Aylesbeare degenerate stand.

▩ *Calluna* ▨ *Erica cinerea* ▧ *Ulex gallii*

■ *Agrostis curtisii* ☐ *Molinia caerulea*

a) Biomass



b) Relative proportions of species

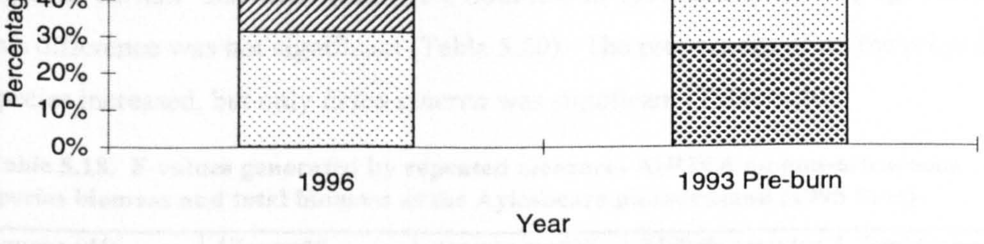


Table 5.17 Flowering performance of *Erica cinerea* in 1996 at the Aylesbeare degenerate stand. Values are means ± 1 SE

	Variable	n	Mean
Flowering Shoots	Biomass (gm^{-2})	8	172.2 ± 41.6
	Density (m^{-2})	8	340.4 ± 71.7
Non-flowering shoots	Biomass (gm^{-2})	8	3.4 ± 2.2
	Density (m^{-2})	8	58.7 ± 35.1
All shoots	Biomass (gm^{-2})	8	175.7 ± 41.8
	Density (m^{-2})	8	399.1 ± 76.4
Non-flowering shoots	Height (cm)	4	6.54 ± 1.00
Flowering shoots	Height (cm)	8	18.8 ± 2.3
	Number of flowers per shoot	8	87.6 ± 25.6
	Number of flowers per infloresence	8	7.93 ± 1.32
	Number of infloresences per shoots	8	9.37 ± 2.75

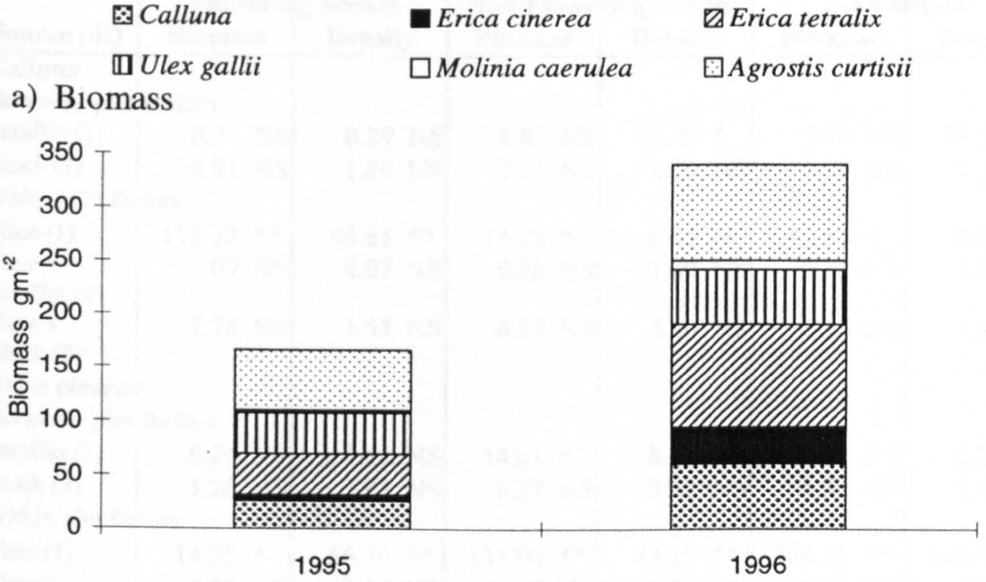
Experiment 2. 1995 Fires

The addition of paraffin had no effect on biomass of regenerating plants (Tables 5.18 and 5.19). Pre-burn biomass was not sampled because these plots were in the same stand of vegetation as the plots burnt in 1994. The total regrowth biomass more than doubled between 1995 and 1996 (Fig. 5.8a), from around 160 g m^{-2} to 340gm^{-2}. The biomass of the ericaceous species increased significantly over time (Table 5.19) but *Ulex gallii*, *Agrostis curtisii* and *Molinia caerulea* were not significantly different between the two years (Table 5.18). The proportions of *Agrostis curtisii* and *Ulex gallii* were both less in 1996 than in 1995 (Fig. 5.8b) but this difference was not significant (Table 5.20). The proportions of all the ericaceous species increased, but only *Erica cinerea* was significant (Table 5.20).

Table 5.18. F-values generated by repeated measures ANOVA on non-ericaceous species biomass and total biomass at the Aylesbeare mature stand (1995 fires)

Source (df)	*Ulex gallii*	*Agrostis curtisii*	*Molinia caerulea*	*Total biomass*
Parffin (1)	0.32 NS	1.11 NS	0.72 NS	0.03 NS
Block (3)	0.26 NS	6.54 NS	2.20 NS	1.22 NS
Time (1)	3.69 NS	4.72 NS	2.99 NS	12.65 *
Time x Fuel (1)	6.77 NS	0.75 NS	0.41 NS	0.01 NS
Time x Block (3)	2.36 NS	1.10 NS	0.45 NS	0.27 NS

Fig. 5.8. Biomass composition of regenerating vegetation after 1995 fires at the Aylesbeare mature stand.


a) Biomass

b) Relative proportions of species

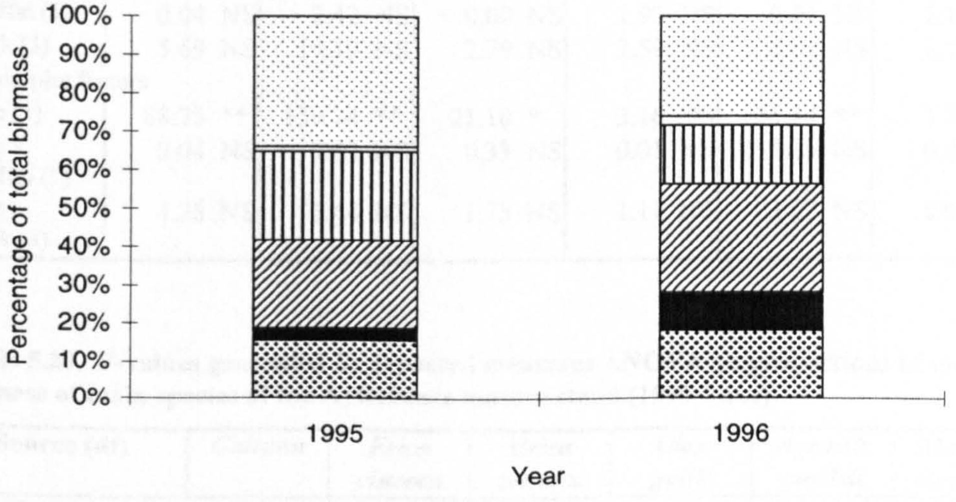


Table 5.19. F-values generated by repeated measures ANOVA on biomass variables of ericaceous species at the Aylesbeare mature stand (1995 Fires)

	Flowering Shoots		Non-Flowering Shoots		All shoots	
Source (df)	**Biomass**	**Density**	**Biomass**	**Density**	**Biomass**	**Density**
Calluna						
Between- plot factors						
Paraffin (1)	0.04 NS	0.29 NS	1.83 NS	13.49 *	1.30 NS	11.56 *
Block (3)	4.81 NS	1.89 NS	2.03 NS	8.72 NS	1.99 NS	7.75 NS
Within-plot factors						
Time (1)	111.32 **	44.61 **	14.02 *	0.01 NS	15.57 *	0.07 NS
Time x Paraffin (1)	3.09 NS	0.07 NS	0.98 NS	1.00 NS	0.59 NS	1.10 NS
Time x Block (3)	7.78 NS	1.53 NS	0.37 NS	4.80 NS	0.46 NS	4.95 NS
Erica cinerea						
Between- plot factors						
Paraffin (1)	0.24 NS	2.85 NS	14.04 *	8.22 NS	6.72 NS	9.25 NS
Block (3)	1.20 NS	2.92 NS	6.27 NS	3.82 NS	4.32 NS	5.51 NS
Within-plot factors						
Time (1)	14.05 *	56.76 **	131.00 **	43.29 **	309.21 **	100.48 **
Time x Paraffin (1)	0.00 NS	0.05 NS	1.47 NS	3.40 NS	9.16 NS	5.60 NS
Time x Block (3)	1.07 NS	2.29 NS	4.89 NS	4.15 NS	11.31 *	11.99 *
Erica tetralix						
Between- plot factors						
Paraffin (1)	0.04 NS	2.42 NS	0.00 NS	1.97 NS	0.01 NS	2.19 NS
Block (3)	5.69 NS	19.19 NS	2.79 NS	2.59 NS	3.87 NS	2.81 NS
Within-plot factors						
Time (1)	88.75 **	159.74 **	21.10 *	3.16 NS	35.34 **	1.34 NS
Time x Paraffin (1)	0.04 NS	0.83 NS	0.33 NS	0.01 NS	0.15 NS	0.00 NS
Time x Block (3)	4.26 NS	6.44 NS	1.73 NS	1.11 NS	2.02 NS	0.95 NS

Table 5.20. F-values generated by repeated measures ANOVA on proportions of total biomass of main species at the Aylesbeare mature stand (1995 Fires)

Source (df)	***Calluna***	***Erica cinerea***	***Erica tetralix***	***Ulex gallii***	***Agrostis curtisii***	***Molinia caerulea***
Paraffin (1)	0.10 NS	7.55 NS	0.20 NS	0.10 NS	0.94 NS	1.98 NS
Block (3)	1.93 NS	0.83 NS	3.02 NS	0.41 NS	6.81 NS	1.94 NS
Time (1)	0.12 NS	22.47 *	1.06 NS	3.30 NS	4.36 NS	1.52 NS
Time x Paraffin (1)	0.59 NS	0.06 NS	0.11 NS	0.19 NS	0.09 NS	0.14 NS
Time x Block (3)	1.61 NS	2.50 NS	0.99 NS	1.21 NS	0.98 NS	0.27 NS

Figures 5.9 and 5.10 show the partioning of the ericaceous species' regrowth into non-flowering and flowering shoots. The two paraffin treatments are shown, because there were some significant differences. The means given below are means of pooled data for variables that had no significant treatment differences.

The biomass of *Calluna* shoots was significantly different between the two years (Table 5.19), increasing from 25 gm^{-2} (2% in flower) in 1995 to 60 gm^{-2} (13% in flower) in 1996 (Fig. 5.9a). There was no difference between the fire treatments in the biomass or density of flowering shoots, but the density of non-flowering shoots as well as total shoot density was significantly different (Table 5.19). Separate analyses of the two sampling periods revealed a significant difference in 1996 but not in 1995 (Table 5.21).

Table 5.21. F-values generated by ANOVA on biomass variables of ericaceous species at the Aylesbeare mature stand (1995 fires) one and two growing seasons after burning, showing treatment (T) and block (B) effects.

		Calluna		***Erica cinerea***		***Erica tetralix***	
Variable		**1995**	**1996**	**1995**	**1996**	**1995**	**1996**
Biomass of flowering shoots	T	1.03 NS	0.59 NS	0.05 NS	0.07 NS	0.02 NS	0.04 NS
	B	3.19 NS	8.46 NS	0.32 NS	1.77 NS	0.34 NS	4.94 NS
Density of flowering shoots	T	0.27 NS	0.21 NS	6.25 NS	1.36 NS	0.02 NS	1.55 NS
	B	1.68 NS	2.10 NS	4.24 NS	2.50 NS	0.24 NS	12.11 *
Biomass of non-flowering shoots	T	1.16 NS	1.59 NS	9.48 NS	22.02 *	0.15 NS	0.05 NS
	B	7.10 NS	0.73 NS	5.16 NS	9.72 *	1.20 NS	3.12 NS
Density of non-flowering shoots	T	3.26 NS	44.25 **	7.63 NS	7.85 NS	0.84 NS	10.45 *
	B	7.21 NS	8.16 NS	3.06 NS	4.20 NS	1.47 NS	12.81 *
Biomass of all shoots	T	1.10 NS	1.04 NS	9.53 NS	3.30 NS	0.15 NS	0.02 NS
	B	6.43 NS	0.92 NS	5.26 NS	4.26 NS	1.20 NS	4.10 NS
Density of all shoots	T	3.18 NS	30.43 *	7.67 NS	9.71 NS	0.84 NS	14.22 *
	B	7.17 NS	5.82 NS	3.09 NS	7.49 NS	1.48 NS	16.04 *

There was no significant difference in total shoot density between the two sampling periods, although the density of flowering shoots increased (Table 5.19 and Fig. 5.10a). There was no difference in flowering performance between the two years, but the height of the non-flowering shoot increased significantly (Table 5.22).

Figure 5.9. Regrowth biomass of ericaceous species after 1995 fires at the Aylesbeare mature stand. -para = no paraffin added, +para = 0.75 l per plot of paraffin added.

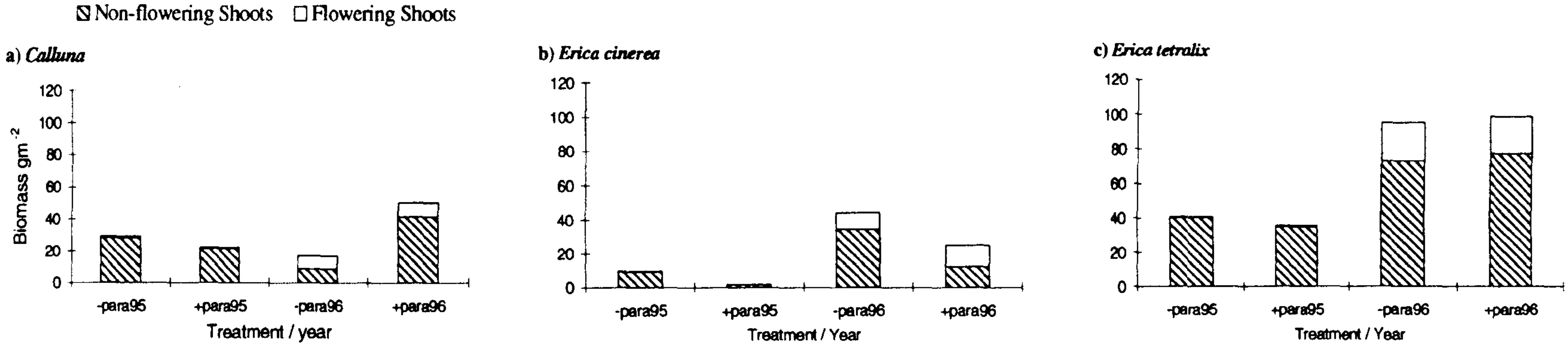


Figure 5.10. Shoot densities of ericaceous species after 1995 fires at the Aylesbeare mature stand

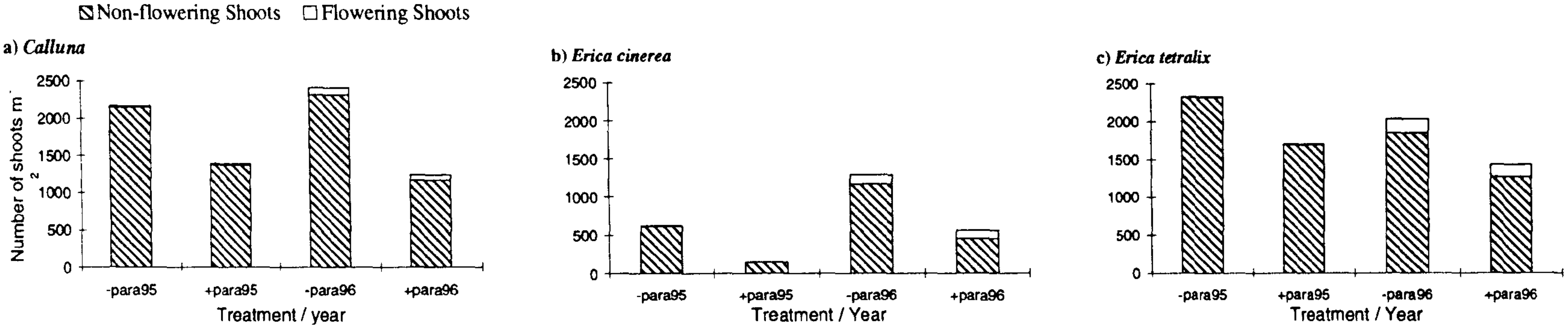


Table 5.22. Performance of ericaceous species in 1995 and 1996 at the Aylesbeare mature stand (1995 Fires). Values are means ± 1 SE. F = results of repeated measures ANOVA, showing the significance of time. None of the other sources of variation was significant.

Variable	n	1995	n	1996	F
Calluna					
Height of non-flowering shoots (cm)	8	3.34 ± 0.10	8	5.34 ± 0.36	491.46 ***
Height of flowering shoots (cm)	8	7.65 ± 0.72	8	9.40 ± 0.61	5.99 NS
Number of flowers per shoot	8	10.97 ± 3.31	8	11.02 ± 1.32	3.28 NS
Number of flowers per infloresence	8	10.97 ± 3.31	8	8.78 ± 0.89	0.49 NS
Number of infloresences per shoot	8	1.00 ± 0.00	8	1.20 ± 0.05	10.04 NS
Number of flowers m^{-2}	8	118 ± 38.4	8	945 ± 256	9.95 NS
Erica cinerea					
Height of non-flowering shoots (cm)	8	3.39 ± 0.19	8	4.81 ± 0.51	15.98 *
Height of flowering shoots (cm)	4	8.13 ± 0.81	7	8.08 ± 1.09	3.51 NS
Number of flowers per shoot	4	2.63 ± 0.75	7	4.83 ± 0.66	9.39 NS
Number of flowers per infloresence	4	2.63 ± 0.75	7	3.70 ± 0.32	2.69 NS
Number of infloresences per shoot	4	1.00 ± 0.00	7	1.31 ± 0.05	4.87 NS
Number of flowers m^{-2}	4	18.75 ± 8.98	7	758 ± 285	19.82 *
Erica tetralix					
Height of non-flowering shoots (cm)	7	4.06 ± 0.08	8	6.19 ± 0.32	10.95 *
Height of flowering shoots (cm)	6	7.06 ± 0.46	8	11.47 ± 0.74	10.64 *
Number of flowers per shoot	6	3.74 ± 1.31	8	7.98 ± 0.50	34.38 **
Number of flowers per infloresence	6	3.74 ± 1.31	8	7.02 ± 0.40	9.41 NS
Number of infloresences per shoot	6	1.00 ± 0.00	8	1.15 ± 0.04	3.21 NS
Number of flowers m^{-2}	6	30 ± 12.2	8	1434 ± 261	115.26 **

Although there was no significant difference between burning treatments in total shoot biomass of *Erica cinerea*, the biomass of non-flowering shoots was significantly greater after burning without paraffin than burning with paraffin (Fig. 5.9b, Table 5.19). Total shoot biomass increased significantly by 30gm^{-2} between 1995 and 1996. There were no significant differences between treatments in shoot densities, and the mean of both treatments increased from 400m^{-2} to 900m^{-2} (Fig

5.10b). Flowering in 1995 was sparse, with only 3% of the biomass in flower. The biomass and density of flowering shoots increased significantly by 1996 (Table 5.19), producing a significant increase in the number of flowers m^{-2} (Table 5.22).

Erica tetralix was the most abundant species by biomass. The standing biomass at the end of the first growing season was almost 40 gm^{-2} in both treatments. The biomass increment between 1995 and 1996 was about 50 gm^{-2} (Fig. 5.9c). There was no overall effect of paraffin on any of the variables (Table 5.19). However, there were significant treatment and block effects on the density of non-flowering shoots and density of all shoots in 1996 (Table 5.21). The biomass of both flowering and non-flowering shoots was significantly different between the two years (Table 5.19). Total shoot density was not significantly between treatments or between years (Table 5.19). There was a significant increase in the density of flowering shoots. In 1995, less than 1% of the shoots were in flower, compared with 10% in 1996 (Fig. 5.10c). There was a significant increase in shoot height and the number of flowers per shoot. The number of flowers m^{-2} was more than 1000 m^{-2} in 1996 (Table 5.22).

5.3.3. Rabbit activity

The density of rabbit pellets was greatest in the plots burnt in 1994 at the Aylesbeare mature stand (Table 5.23). There was a significant difference between stands (one-way ANOVA, $F = 12.08$, $p < 0.001$, 4df). Calculation of the least significant difference using Bonferroni's adjustment gave a value of 5.92 for 10 comparisons with 35 error degrees of freedom. The plots burnt in 1994 at the Aylesbeare mature stand were significantly different from all other stands except the neighbouring plots burnt in 1995. These plots were significantly different from the two stands at Arne but not from the Aylesbeare degenerate stand. Rabbit activity was very low at both stands at Arne and in the degenerate stand at Aylesbeare. There were no significant differences between these three stands.

Table 5.23. Rabbit activity at all stands. Values are means of the number of droppings ± 1 SE of 8 burnt plots at each stand. Ten quadrats of $0.04m^2$ were sampled in each plot.

Site / Stand	Number of pellets / quadrat
1994 Fires	
Arne Mature	0.53 ± 0.108
Arne Degenerate	0.64 ± 0.118
Aylesbeare Mature	11.53 ± 2.55
Ayesbeare Degenerate	2.44 ± 1.20
1995 Fires	
Aylesbeare Mature	7.70 ± 1.34

5.4. Discussion

5.4.1. Effect of fire temperature and stand age on post-fire regeneration

Vegetative regeneration of *Calluna* was more successful at both the mature stands than at the degenerate stands. This decline in resprouting ability with pre-burn age of the stand is in agreement with previous work in Scotland (e.g. Kayll and Gimingham, 1965; Grant, 1968; Hobbs and Gimingham, 1984b). However, both the mature stands at Arne and Aylesbeare were more than 20 years old when burnt and the degenerate stands were thought to have been unburnt for at least 40 years. It appears that the capacity to regenerate may decline less rapidly than it does in Scotland. For example, Kayll and Gimingham (1965) observed a rapid decline in resprouting from the age of 15 years, but Miller and Miles (1970) and Hobbs and Gimingham (1984b) found a steady decrease in the rate of regeneration with pre-burn age and no evidence of a steep decline. Hobbs and Gimingham (1984b) reported virtually no regeneration of either *Calluna* or *Erica cinerea* from mature stands of 14 - 27 years of age. However, Grant (1968) noticed satisfactory regeneration from stands up to 20 - 25 years of age.

The fire temperatures generated by the fuel load treatments had no effect on regeneration after the 1994 fires at any of the stands. Although fire temperatures were significantly different between fuel load treatments (except at the degenerate stand at Aylesbeare), the range of temperatures in such management fires were probably not sufficient to elicit a significant difference in vegetation response. Hobbs and Gimingham (1984b) suggested that the pre-burn age of the stand has more influence than fire temperature on post-fire regeneration because fire severity is itself influenced by stand age and structure. In this study, fires of similar fuel loads produced similar temperatures at the two stands at Arne (Chapter Three), thus the differences in regeneration were entirely due to differences in resprouting capacity rather than temperature. Fires at the degenerate stand at Aylesbeare were considerably cooler than at any other stand, but *Calluna* still failed to resprout. Therefore the lack of regeneration after burning degenerate *Calluna* was not due to high temperatures killing rootstocks and regeneration buds (Kenworthy, 1963). Instead, these results are consistent with the findings of Mohamed and Gimingham (1970) and Miller and Miles (1970), that the ability of *Calluna* to resprout declines with age due to lignification of regeneration buds and a lower density of regeneration centres in degenerate stands.

The addition of paraffin to plots burnt in 1995 did not generate higher temperatures than plots burnt without paraffin (Chapter Three). There were no gross effects of paraffin on regeneration, but the ericaceous species showed treatment effects on the number and / or biomass of non-flowering shoots. Although significant, in view of the lack of any effect on the number or biomass of flowering shoots, this effect was subtle. It may be a random effect related to the site location of treated plots, or paraffin may have altered resprouting of ericaceous species by an unknown mechanism. The aim of this work is not to elucidate the effects of paraffin on plant regeneration, so the general effects of burning on vegetative regeneration will be discussed and compared with the first burning experiment.

5.4.2. Species composition and succession

Despite the slow regeneration at the degenerate stands, there was no invasion by ‘undesirable’ species such as pine, birch or bracken in the three years of monitoring. By the end of the third growing season after burning there was more than 60% cover of vegetation at the degenerate stand at Aylesbeare. Extensive areas of bare ground persisted at the degenerate stand at Arne, but few herbaceous species or bryophytes were observed. This may have been due to the lack of a nearby source of propagules coupled with the unsuitable micro-environment of persistent bare ground for the establishment of both invasive species and ericaceous species (Mallik and Gimingham, 1983). The bushes of ericaceous species that had regenerated at this stand were growing vigorously in the absence of competition. Accompanied by seedling establishment, cover of ericaceous species should eventually develop at this stand. However, species composition may shift in favour of *Erica cinerea* or *Erica tetralix*. Both species were present at low cover in the pre-burn vegetation (*E. tetralix* in one block only) but contributed more than *Calluna* to the biomass of the regenerating vegetation.

Regeneration at the mature stand at Arne was successful in that *Calluna* resprouted rapidly from rootstocks and the percentage of bare ground decreased rapidly. *Erica cinerea* and *Ulex minor* were scarce but were infrequent before burning. There were some *Pinus sylvestris* seedlings and fronds of *Pteridium aquilinum*, but there was no evidence of invasion by species not present in the pre-burn vegetation.

At both stands at Aylesbeare, *Calluna* was relatively less frequent after burning than before. The change in vegetation composition was marked at the degenerate stand, where *Calluna* failed to resprout and *Erica cinerea*, *Ulex gallii* and *Agrostis curtisii* were co-dominant three growing seasons after burning. Both *Agrostis curtisii* and *Molinia caerulea* were relatively more abundant in the regenerating vegetation than they were before burning. Unlike *Calluna*, resprouting of *Erica cinerea* seems to be unaffected by the age of the plant before burning. This disagrees with Hobbs, Mallik and Gimingham (1984), who found that the resprouting capacity of *Erica cinerea* also declined with age.

There was little change in the relative proportions of species in the first two growing seasons after burning at the Aylesbeare mature stand. *Erica tetralix* resprouted more vigorously than either *Calluna* or *Erica cinerea*. Shoot height, density and biomass of this species were all greater than in the other two ericaceous species. *Agrostis curtisii* and *Ulex gallii* were co-dominant with *Erica tetralix* at this stand and all three increased significantly in biomass over the recording period. The resprout frequency of *Erica tetralix* also increased throughout the monitoring period, but *Agrostis curtisii* and *Ulex gallii* did not show a similar response. In the third growing season, the relative proportions of *Agrostis curtisii* and *Ulex gallii* decreased as the proportions of *Erica tetralix* and *Calluna* increased, implying a succession towards the dominance of ericaceous shrubs. However, this is only an early phase of succession, and a longer period of study is required to determine whether these trends are directional.

Regeneration after burning in 1995 at the Aylesbeare mature stand showed some differences from the neighbouring plots which were burnt in 1994. Although *Erica tetralix*, *Agrostis curtisii* and *Ulex gallii* were still co-dominant, *Erica cinerea* and *Calluna* resprouted more vigorously and made a larger contribution to the total biomass than they did in the plots burnt in 1994. All three ericaceous species increased in percentage contribution to the total biomass (but only *Erica cinerea* was significant), whereas *Ulex gallii* and *Agrostis curtisii* showed a proportional decline. The resprout frequency data from this experiment showed an upward trend for *Erica tetralix* only. The frequencies of *Agrostis curtisii* and *Molinia caerulea* did not change significantly over the recording period but all other species showed a significant decrease. There must have been some mortality of resprouts between 1995 and 1996 although biomass continued to increase due to continuing growth of the surviving shoots. Given that these plots were in the same stand of vegetation, the differences in post-fire successsion must be due to some factor(s) exerting an influence after burning. Differences in weather and grazing are possible factors. The drought of 1995 may have affected regeneration in the two experiments in different ways depending on the time of burning. Rabbit activity, as measured by the number of pellets, was not significantly different between the two sets of plots, but rabbit burrows were adjacent to the plots burnt in 1994 and many plants showed signs of grazing. Both *Calluna* and *Erica cinerea* often exhibited dense cushion-like growth typical of heavy grazing (Grant and Hunter, 1966). Grant (1968) noted that *Calluna* was grazed in preference to *Erica tetralix* and that when a low cover of young *Calluna* was grazed by sheep, development of many lateral shoots was encouraged, producing a prostrate morphology.

The abundance of herbaceous species (in this case, *Agrostis curtisii*) after burning at Aylesbeare and the delayed increase in ericaceous species is similar to successional trajectories observed in Scotland (e.g. Legg, 1980; Gimingham, Hobbs and Mallik, 1981; Mallik and Gimingham, 1983, Hobbs and Gimingham, 1984b) and after severe fires on Dorset heathland (Gray, 1988). These workers found that herbaceous species were temporarily dominant after burning before ericaceous species began to attain dominance. However, Scottish studies also distinguished a peak in bryophytes and lichens, which was not evident in this study.

All stands were typical of an initial floristic composition model of succession (Egler, 1953; cited in Connell and Slatyer, 1977), with species present in the pre-burn community regenerating immediately after burning (Gimingham, Hobbs and Mallik, 1981). The changes in relative abundances of species at Aylesbeare may be due to individualistic responses of species to environmental factors such as drought and grazing (Pickett and McDonnell, 1989). The competitive abilities of the different species may change as the vegetation develops (*sensu* the 'resource ratio' hypothesis of Tilman, 1988).

5.4.3. Regrowth Biomass and Production

Litter fall and herbivory were not measured, so the increment in regrowth dry weight over the recording period could not strictly be used to estimate total above-ground production. However, production of litter and wood (lignified shoots) are negligible in the first few years after burning (Gimingham, 1972), thus, in the absence of grazing, shoot growth closely approximates to above-ground production. Although the amount of plant material removed by herbivory was not assessed, there was no evidence of grazing at the mature stand at Arne. At the mature stand at Aylesbeare, however, rabbit activity was high and many plants showed signs of grazing. Therefore the results from Arne can be compared with previous work, but it is important to bear in mind that the first sample was taken only 6 months after burning and the two subsequent samples at annual intervals. However, if growth was negligible over the winter, then the increments in biomass can be regarded as the increase over each growing season.

Chapman (1967) estimated net above-ground production of *Calluna* in Dorset at 1200 kg ha^{-1} y^{-1} (= 120 gm^{-2}y^{-1}) for the first ten years following burning. The production of the first two growing seasons at Arne was very similar to this, at 108.7 gm^{-2} and 120 gm^{-2} in the first and second growing seasons respectively. Between 1995 and 1996, production was four times greater, at about 425 gm^{-2}. The standing crop of Dorset heath calculated by Chapman *et al.* (1975a) was 158 gm^{-2} for all species one year after burning (*Calluna* was 88 gm^{-2}). Biomass more than doubled in the second growing season, but remained quite stable in the third. These results are quite different to those found in this study, where production peaked in the third growing season after burning. These differences in dry matter production are probably due to year - to -year variation in weather, particularly the drought of 1995.

The biomass increment between sampling periods at the mature stand at Aylesbeare was limited by rabbit grazing. Total production by all species at the Aylesbeare mature stand was consistent over the recording period, at about 150 g m^{-2}y^{-1}, although ericaceous species showed little increase in biomass between 1994 and 1995. The biomass of *Erica tetralix* only increased by 9.4 gm^{-2} between 1994 and 1995, compared with 55gm^{-2} in the first growing season after burning and 88 gm^{-2} in the third year. The low rainfall of 1995 may have limited production of this species. Both *Calluna* and *Erica cinerea* showed no significant increase in biomass between 1994 and 1995, probably due to both drought and selective grazing of these species.

The addition of paraffin in the 1995 fires at the Aylesbeare mature stand had no effect on biomass increment. Total production in these plots was similar to the neighbouring plots burnt in 1994, at about 170 gm^{-2} y^{-1}. Although production by the ericaceous species was lower in the first growing season after burning than in the second, the biomass increment of all three species from the time of burning at the end of March 1995 to the time of sampling at the end of September was greater than that shown over a whole year by the neighbouring plots burnt in 1994. Therefore there is no evidence of drought affecting production in this experiment.

5.4.4. Shoot density of ericaceous species

Changes in the shoot density of the ericaceous species indicate whether increases in biomass were due to the emergence of new shoots or the growth of existing shoots. The density of regenerating shoots depends on the pre-burn age of the stand because pre-burn stem density and post-fire resprout density are correlated (Hobbs, Mallik and Gimingham, 1984). At the Arne mature stand, the density of *Calluna* shoots was highest at the end of the first growing season after burning. Less than 1% of these shoots were in flower, and the non-flowering shoots were only 5cm tall. Individual shoots were not tagged, but it appears that nearly 50% mortality occurred between September 1994 and September 1995. This mortality may have been due to density-dependent factors (self-thinning) or as a result of the 1995 drought. Shoot density increased by the end of the third growing season in 1996, but the percentage increase in density was not as large as the percentage increase in biomass. Therefore above-ground production was due mainly to the growth of existing shoots rather than the appearance of new shoots.

At the Aylesbeare mature stand, the productivity of *Erica tetralix* was entirely due to the growth of surviving shoots, because the shoot density did not change significantly over the recording period. This implies that *Erica tetralix* invested energy in growth of shoots which emerged soon after burning, rather than the production of new shoots. The shoot biomass and density of *Calluna* were much lower than those of *Erica tetralix,* but also showed a significant increase in biomass but no significant increase in shoot density. *Erica cinerea* appeared to be the most heavily grazed of the ericaceous species, because neither the biomass nor the density of shoots increased significantly over the recording period. *Calluna* is more tolerant to grazing than *Erica cinerea* (Gimingham, 1949) and *Erica tetralix* is avoided (Grant, 1968). Herbivory by rabbits has been found to limit growth, flowering and seed-set of *Erica cinerea* in burned grasslands in Brittany (Forgeard and Chapuis, 1984).

5.4.5. Flowering

Fire temperature had little effect on the production of flowers. The only significant difference between fuel load treatments was in the density and biomass of flowering shoots in 1994. This was probably a random effect, because flowering was very sparse. In samples of $0.1m^2$, there were means of only 5 shoots in the low fuel load treatment, and 1.9 shoots in the high fuel load treatment.

At the Arne mature stand, *Calluna* flowered prolifically in the second and third growing seasons after burning. The number of flowers per infloresence, infloresences per shoot and shoot density all increased over time. In 1996, there were more than 70000 flowers per m^2. This represents only three growing seasons of biomass accumulation and is higher than some counts made on more mature stands of *Calluna*. For example, Miller (1979) counted 54000 *Calluna* flowers m^{-2} in Scotland and Traynor (1995) found 56000 m^{-2} in mature *Calluna*-dominated vegetation at Arne. Legg, Maltby and Proctor (1992) estimated 114000 flowers m^{-2} in an ungrazed area of the North York Moors.

The three ericaceous species at the mature stand at Aylesbeare differed in their flowering performance after burning, again probably due to selective grazing. Flowering of *Erica tetralix* was more prolific than either *Calluna* or *Erica cinerea.* The last two species did not flower in the first growing season after burning and *Erica tetralix* produced three times more flowers per unit area in 1996 than the other two species put together, with over 5000 flowers m^{-2}. This was due to the production of many flowering shoots rather than branching of existing shoots.

Flowering and growth of *Calluna* and *Erica cinerea* in the two growing seasons after the 1995 fires at the mature stand at Aylesbeare was far more successful than in the same period after fires in 1994. All three ericaceous species flowered in the first growing season after burning. *Erica tetralix* resprouted most vigorously but produced less flowers than *Calluna* in 1995. The number of *Calluna* flowers per unit area was not quite significantly different between the two years, whereas *Erica tetralix* flowering was more abundant in 1996 than in 1995.

Regeneration at the degenerate stands was sampled only once, three growing seasons after burning. Although regeneration was sparse at the Arne degenerate stand, the bushes that were resprouting were growing vigorously. Flowering shoots of all species were more than 20cm tall and branching was extensive. *Calluna* produced a mean of nearly 170 flowers per shoot. *Calluna* did not regenerate at the Aylesbeare degenerate stand. However, *Erica cinerea* resprouted and flowered successfully.

5.4.6. Conclusions

There was no effect of temperature on regeneration over the range of fuel loads tested. Only *Calluna* showed a decline in ability to resprout with age. Other ericaceous species, where present in the degenerate stands, resprouted from rootstocks. The lack of rabbit grazing at the mature stand at Arne enabled more vigorous resprouting and flowering at this stand than at the corresponding stand at Aylesbeare. Weather, soil nutrients and grazing pressure probably interact in their influence on production. Further work on the impact of grazing on species composition and production is required, especially if burning is to be used to re-habilitate an area followed by grazing management.

The succession after burning at all stands was characterised by the floristic compostion before burning. There was evidence of changes in the relative abundances of species at Aylesbeare; however, with ericaceous species beginning to increase relative to *Agrostis curtisii* and *Ulex gallii* by the end of the recording period (2.5 years after burning). The contribution of seedling establishment to post-fire succession is described in Chapter Six, and would be expected to have more influence at the degenerate stands, particularly at Arne. Despite the persistence of bare ground after burning the degenerate stand at Arne, there was no invasion of woody colonising species or bracken. Hence there is no reason to discourage the use of burning as a method for managing degenerate heath on large sites where there are few propagules of invasive species.

CHAPTER SIX

Demography of ericaceous seedlings after burning

6.1. Introduction

The relative contributions of seedling establishment and resprouting to regeneration after burning heathland depend chiefly on the age of the stand that is burnt (Chapter Five, Hobbs and Gimingham, 1984a, Miller and Miles, 1970). Vegetative regeneration after burning degenerate heath is usually poor (Chapter Five; Kayll and Gimingham, 1965; Grant, 1968; Miller and Miles, 1970; Mohamed and Gimingham, 1970; Hobbs and Gimingham, 1984), so vegetation recovery may depend on seedling establishment (Hobbs and Gimingham, 1984b; Mallik, Hobbs and Legg, 1984). Seedlings make a negligible contribution to overall biomass when vegetative regeneration is successful, but are the only means of introducing both genetic and structural diversity to even-aged stands (Fernandez-Santos and Gomez Gutiérrez, 1994). Seedlings which germinate at the edges of gaps in resprouting vegetation are subject to different microclimatic conditions to those germinating in the middle of large gaps (Miller and Miles, 1970; Miles, 1974a; de Hullu and Gimingham, 1984). These differences may affect seedling density and survivorship.

Studies by Miles (1972, 1974a and b), Mallik and Gimingham (1985), Mallik, Hobbs and Rahman (1988), and Legg, Maltby and Proctor (1992) have identified some of the factors affecting germination and establishment of heathland species. The physical and chemical characteristics of the soil surface are changed by burning (DeBano, Dunn and Conrad, 1977; Legg *et al.*, 1992). The blackened surface has a low albedo subject to high summer temperatures and a high evaporation rate (Gimingham, 1972; Thomas, 1984, Mallik, Hobbs and Rahman, 1988). The action of burning and the temperature to which the substrate is exposed affect microclimate, water relations and nutrient availability. Burning tends to enhance soil water retention by decreasing infiltration and evapotranspiration but the surface dries rapidly in summer (Mallik, 1982, 1986). Burnt areas are more exposed than the substrate beneath a closed canopy to physical factors such as insolation, precipitation, wind and drought (Whittaker and Gimingham, 1962; Mallik, 1986). The quantity of nutrients lost in smoke increases with fire temperature (Kenworthy, 1963; Evans and Allen, 1971). Mineral nutrients in the ash are readily dissolved and leached through the soil profile but are soon replaced by nutrients in rainfall (Allen, 1964; Allen, Evans and Grimshaw, 1969).

Germination under a dense canopy is rare (Whittaker and Gimingham, 1962; Miles, 1973), but not unknown (deHullu and Gimingham, 1984). Increased illumination stimulates germination of ericaceous species (Gimingham, 1960; Whittaker and Gimingham, 1962; Bannister, 1964; Pons, 1988, 1989; Mather and Williams, 1990) and the germination of *Calluna* is enhanced by a fluctuating temperature regime (Whittaker and Gimingham, 1962). Hence fire is a means of opening the vegetation canopy and encouraging germination. The temperature and intensity of fire may also affect seedling germination and survival. Whittaker and Gimingham (1962) found that charring and temperatures greater than 200°C were lethal to *Calluna* but germination was stimulated by moderate heat. For example, temperatures of 120°C stimulated germination at exposure times of less than 25 seconds, but germination rates rapidly declined at exposure times greater than this. However, subsequent work by Mallik and Gimingham (1985) and González-Rabanal and Casal (1995) found no significant effect. Elevated temperatures may stimulate germination of other heathland species (van de Venter and Esterhuizen, 1988; González-Rabanal and Casal, 1995). Plant-derived smoke has been identified as a factor promoting the germination of some South African fynbos species (Brown, 1993; Baxter and van Staden, 1994; Baxter *et al.* 1994) as well as some Australian species (Dixon, Roche and Pate, 1995). Therefore fire temperature and intensity may affect vegetation if different species respond differently to temperature or have different requirements for germination and establishment (Pannell, 1995).

There have been very few studies comparing survivorship after fires of different intensities, season or size (Whelan, 1995) and no work on the seedling demography of ericaceous species after burning southern lowland heath. This chapter describes a detailed study of the population dynamics of ericaceous seedlings after fires of different temperatures and intensities on both mature and degenerate heath.

The effects of vegetative regeneration of the mature stands on seedling germination and survival are examined and microclimatic data presented.

6.2. Methods

6.2.1 Burning

Experiment 1. 1994 Fires

Mature and degenerate stands of vegetation were selected at two sites: Arne in Dorset and Aylesbeare in Devon (Chapter Two). Twelve plots of 5 x 5 m were laid out in a strip at each stand separated from one another by 3m to minimise ash drift. A randomised block design was used, with four replicate blocks of two burning treatments plus unburnt controls at each stand. The treatments were to burn high and low fuel loads of vegetation. Burning was carried out in March, 1994. The methods of vegetation manipulation and burning are described in Chapter Three. Temperatures were recorded with pyrometers consisting of temperature sensitive paints in strips on tiles.

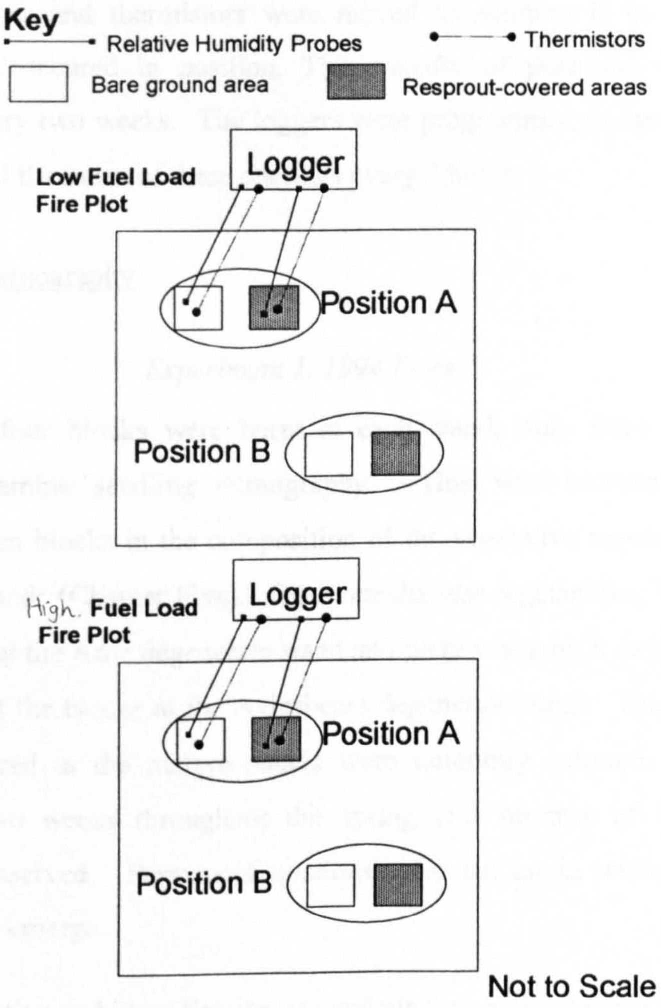
Experiment 2: 1995 Fires

Only the Aylesbeare Mature stand was used for the second experiment in March 1995. A strip of twelve plots of 3m x 2m was set up adjacent to the plots burnt in 1994. A randomised block design of two treatments plus unburnt controls was employed. The two burning treatments were to burn plots sprayed with 0.75 l of paraffin and plots with no added paraffin (Chapter Three). Two methods of temperature recording were used: pyrometers as described above and thermocouples attached to a data logger.

6.2.2. Microclimate Monitoring

Temperature and relative humidity were measured continuously for one year in two plots at Arne Mature. Only two loggers were available so this limited the number of plots that could be monitored. The plots were in the same block and adjacent to one another, chosen for their similar topography and aspect. Two apparently similar areas of bare ground and resprout cover approximately 10 cm apart were selected. Monitoring began in October 1995, two growing seasons after fire, and resprouts were about 10 - 20 cm high. The position of the loggers in the two plots is shown diagrammatically in Figure 6.1.

Figure 6.1. Schematic diagram of microclimate monitoring at Arne



A Squirrel data logger (1000 series, Grant Instruments, Cambridge) with two relative humidity probes and two thermistors was positioned at monitoring point A in each plot. One probe and one thermistor were placed on the litter surface within the bare ground area (Plate 6.1) and the other pair were placed within the resprouting area (Plate 6.2). Each pair of probe and thermistor were secured together with a metal clip inserted in the ground so that their precise positions could be re-located. The loggers, probes and thermistors were moved to position B in both plots a fornight later and secured in position. This transfer of positions was repeated approximately every two weeks. The loggers were programmed to sample every 15 minutes and record the mean of these readings every 2 hours.

6.2.3. Seedling Demography

Experiment 1. 1994 Fires

Although four blocks were burnt at each stand, only three blocks were monitored to examine seedling demography. This was because there were differences between blocks in the composition of the vegetative regeneration at the two degenerate stands (Chapter Five). *Erica tetralix* was regenerating vigorously in one of the blocks at the Arne degenerate stand and there was a high cover of *Molinia caerulea* in one of the blocks at the Aylesbeare degenerate stand. The three blocks that were monitored at the mature stands were randomly selected. Plots were checked every two weeks throughout the spring and summer of 1994 but no seedlings were observed. Permanent quadrats were set up in winter 1994 after seedlings began to emerge.

To aid location and identification of quadrats four parallel strips of 0.2m x 4m were positioned in each plot, avoiding the outermost 0.5 m to reduce edge effects. Each strip was divided into 20 20cm^2 quadrats.

At the mature stands, the effects of resprouting on seedling establishment and survival were investigated by selecting quadrats of low and high resprout cover within each plot (split plot design). The percentage cover of resprouts in the 80

Plate 6.1. Relative humidity probe and thermistor in a 'bare ground area'

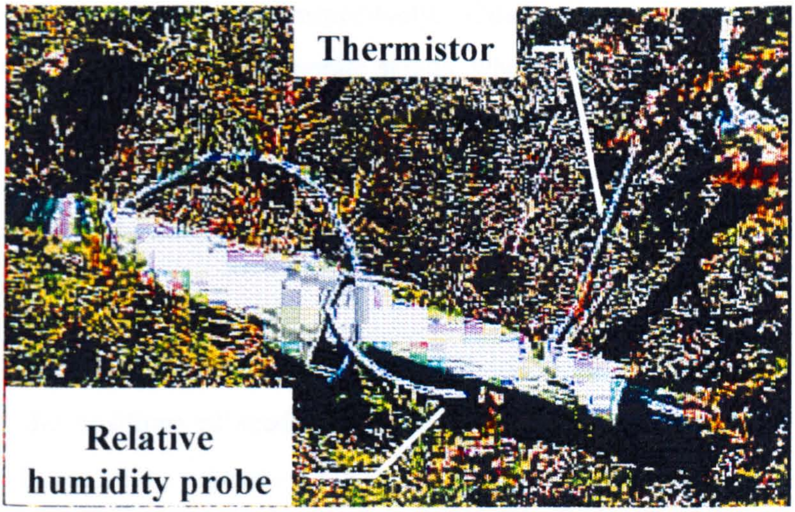


Plate 6.2. Relative humidity probe and thermistor (obscured) in in a 'resprouting area'

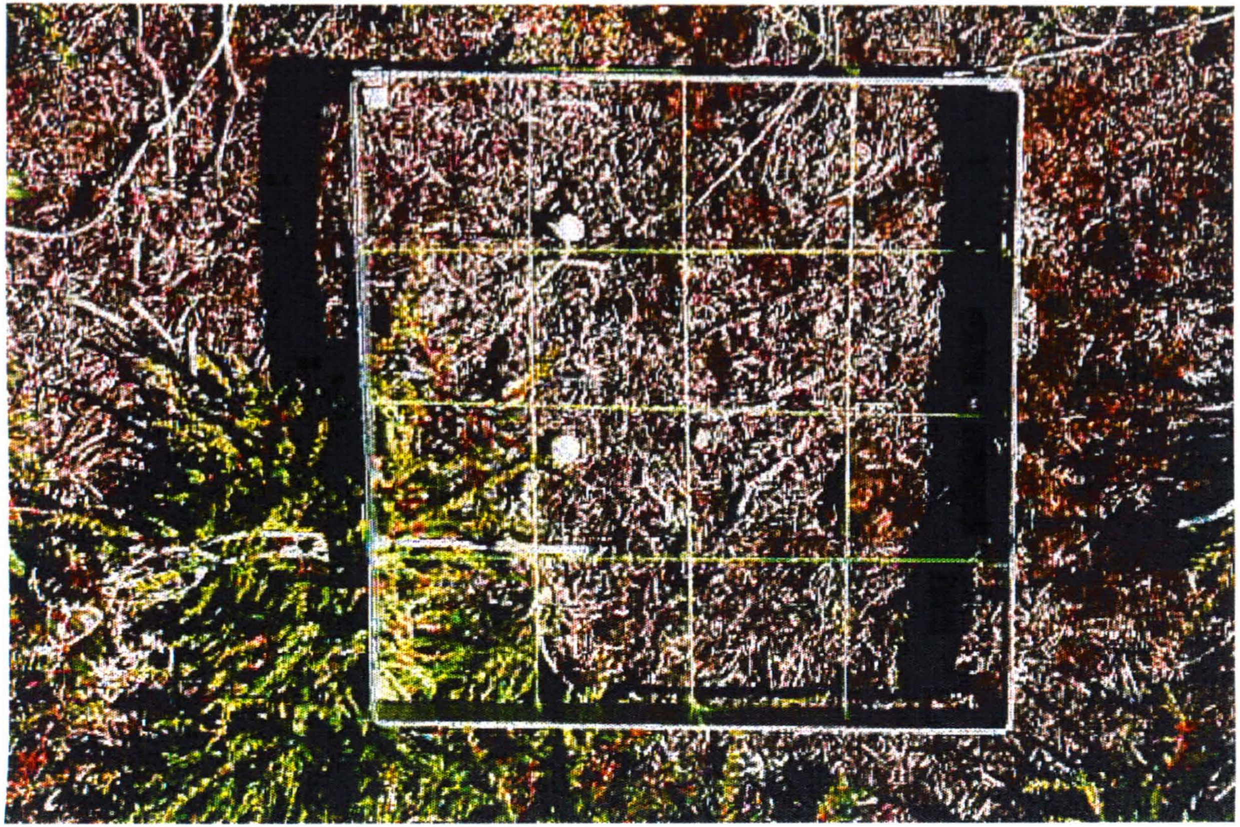
quadrats was assessed. Quadrats of <10% cover and 40 - 70% cover were assigned to low and high cover categories respectively. Quadrats of 10 - 30% and > 70% cover were discarded. At the degenerate stands, where vegetative regeneration was very sparse, all quadrats had less than 10% cover of resprouts. At the first census, quadrats were chosen at random until a minimum of 200 seedlings were mapped for each cover category in each plot. Permanent quadrats were marked at the corners with dowelling pegs.

In all plots a 20 cm^2 aluminium quadrat divided into 16 squares was used to aid mapping the positions of seedlings (Plate 6.3). Seedlings were mapped onto graph paper. Resprouting vegetation and the positions of stones and large twigs were also mapped for seasonal markers. The maps were photocopied after each census and new seedlings appearing at the next census marked with pencil so they could be distinguished from existing seedlings. Seedlings were classified as dead when they had either disappeared or had no green pigment remaining. The emerging seedlings were identified to species when possible, but most died before they were identifiable. Therefore the ericaceous species were pooled for analysis.

The first census was in January - February 1995. Hence the first cohort of seedlings was a cumulative measure of the seedlings that had germinated and died over the first autumn and early winter after fire. Subsequent censuses were in April, July, October, December 1995, and February, April and August 1996. The four stands and the quadrats within them were always monitored in the same order: first the degenerate stands and then the mature stands at Arne and then Aylesbeare. Each census period spanned two to four weeks, depending on the time of year and the number of new seedlings that had emerged.

Monitoring of some quadrats at the mature stand at Arne ceased after the third census. These were quadrats in which the first two cohorts had become extinct and there had been no emergence between the second and the third census. This decision was made during the fourth census, when there were so many new seedlings that it was not practical to continue monitoring all the quadrats. Therefore only quadrats

Plate 6.3. Demography Quadrat



that were mapped throughout the whole monitoring period were used in the population flux analyses but more quadrats were monitored and analysed for the first two cohorts of seedlings than for later cohorts.

Experiment 2. 1995 Fires

Six quadrats of 20 cm^2 were positioned randomly in each plot in July 1995 before seedlings began to germinate. There was no selection of quadrat position based on percent cover of resprouts. Seedlings first appeared in October 1995 (census 2) and quadrats were chosen at random until a minimum of 100 seedlings were mapped in each plot. This experiment was monitored immediately after each census of the 1994 plots, using the same mapping technique.

6.2.4. Data Analysis

Microclimate

Microclimatic variables of relative humidity and mean, minimum and maximum daily temperatures were extracted from the output of the data loggers. These variables were analysed using paired t-tests to compare the bare ground and resprout-covered areas. The two plots were analysed separately.

Seedling Demography

At the mature stands, not all seedlings were under resprouts in high cover quadrats or on bare ground in low cover quadrats. Seedlings were deemed to be affected by resprouts if they were within 10 mm of the aerial cover of the resprouts. Seedlings unaffected by resprouts in high resprout cover quadrats and seedlings affected by resprouts in low cover quadrats were excluded from the survivorship analyses. Seedlings that became affected by resprouts as cover increased over time were also excluded. All seedlings were included in analyses of changes in population density, deaths and recruitment because the area monitored had to remain constant over time. Only quadrats that had been mapped at every census were used in these analyses, but quadrats that were abandoned after census three were used in the survivorship curves of the first two cohorts, as long as both cohorts had become extinct at census three.

Survivorship curves were plotted for each cohort using the subset of seedlings described above. Each cohort consisted of the number of new seedlings that emerged between the designated census and the previous census. The number of seedlings per plot in each cohort was standardised to 1000 so that cohorts could be compared. Survivorship curves were compared using the 'LIFETEST' procedure in SAS (SAS Institute Inc., 1989). This procedure analyses the survivorship data as the 'age at death' for each seedling. Seedlings that were still alive at the end of the monitoring period (August 1996) were entered as 'right-censored' observations (Fox, 1993). 'LIFETEST' computes Wilcoxon and log-rank statistics which test for heterogeneity in the distribution of seedling longevities among treatments (Fox, 1993). SAS uses the $\chi 2$ approximation to these tests and compares the observed with the expected number of deaths in each interval. The Wilcoxon statistic places more weight on earlier survival times and the log-rank statistic on later survival times (SAS, 1989), so comparison of the two values indicates when the survivorship of the populations differs the most. The survivorship curves were analysed for treatment effects within each stand. Hence only two treatments (low and high fuel load) were compared at the degenerate stands, but there were four treatments at the mature stands (low fuel / low cover; low fuel / high cover; high fuel / low cover and high fuel / high cover). If the Wilcoxon and log-rank tests revealed heterogeneity between these four treatments, multiple comparisons were made by calculating Z-statistics from the Wilcoxon and log-rank scores (Fox, 1993).

Population density was calculated from:

$$N_{t+1} = N_t + B - D \qquad (3)$$

where N = seedling density, t = census, B = number of seedlings that emerged m^{-2} between censuses t and $t + 1$ and D = number of seedlings that died m^{-2} between censuses t and $t + 1$ (Silvertown and Lovett-Doust, 1993). Seedling emergence and deaths between censuses and population density at each census were log transformed and analysed using repeated measures ANOVA. The proportional mortality between censuses was calculated by dividing the number of seedlings dying at census $t+1$ by the number of seedlings alive at census t and was analysed by repeated measures ANOVA after arcsine transformation. Section 5.2.6. in Chapter Five describes the procedure of repeated measures ANOVA.

Fuel load treatments were compared at the degenerate stands. A split plot design was appropriate at the mature stands with resprout cover the subplot factor and fuel load treatment and blocks as the main plot factors. To test for any differences between stand age in response to fuel load treatments the degenerate stands were compared with the low resprout cover category of the mature stands using nested repeated measures ANOVA.

6.3. Results

6.3.1. Burning

Experiment 1. 1994 Fires

The results of burning high and low fuel loads at mature and degenerate heath at both sites are described in Chapter Three. Table 3.5 from Chapter Three is repeated as Table 6.1 to show the mean temperatures that were recorded. Fires in the high fuel load treatments were significantly hotter and more intense than the fires in the low fuel load treatments (Table 6.1). The Aylesbeare degenerate stand was the exception, where all the fires were comparatively cool. Above-ground temperatures were higher then the temperatures on the litter surface, with maxima of 400 - 500°C in high fuel load fires (Table 6.1).

Table 6.1. Mean maximum fire temperatures at soil and litter surfaces and above-ground (0-14cm) in 1994 fires. Values are means ± standard errors with the range of values in parentheses. S = Friedman Statistic comparing fuel load treatments. NS = not significant, * = 0.01 < p < 0.05

Site / Stand	Vertical Position	Temperature (°C) Low fuel	Temperature (°C) High fuel	S
Arne Mature	Soil Surface	39.8 ± 6.5 (5 - 62)	64.6± 23.6 (5 - 204)	1.00 NS
	Litter Surface	81.0 ± 13.5 (38 - 204)	162.8 ± 70.3 (38 - 704)	4.00 *
	Above-ground	393.0 ± 81.9 (135 - 1038)	581.4 ± 67.0 (204 - 704)	4.00 *
Arne Degenerate	Soil Surface	9.8 ± 4.8 (5 - 62)	36.7 ± 15.4 (5 - 101)	3.00 NS
	Litter Surface	48.3 ± 11.9 (5 - 101)	112.3 ± 23.3 (62 - 246)	4.00 *
	Above-ground	173.9 ± 31.1 (62 - 204)	444.8 ± 8.2 (343 - 704)	4.00 *
Aylesbeare Mature	Soil Surface	15.3 ± 7.1 (5 - 62)	54.3 ± 13.6 (5 - 135)	4.00 *
	Litter Surface	32.75± 9.86 (5 - 87)	88.7 ± 19.8 (38 - 204)	4.00 *
	Above-ground	178.1 ± 8.07 (62 - 343)	396.2 ± 77.9 (149 - 704)	4.00 *
Aylesbeare Degenerate	Soil Surface	5.0 ± 0.0 no paints melted	5.0 ± 0.0 no paints melted	0.00 NS
	Litter Surface	19.17 ± 6.22 (5 - 62)	21.93 ± 5.93 (5 - 62)	0.33 NS
	Above-ground	207.9 ± 57.6 (62 - 704)	154.75 ± 7.39 (101 - 204)	0.00 NS

Experiment 2: 1995 Fires

There was no significant difference in mean temperature between the two treatments (+ / - paraffin). Fire temperatures recorded by pyrometers and thermocouples are shown in Table 6.2 (Table 3.10 in Chapter Three). Pyrometers recorded mean litter surface temperatures of 200 - 300°C and above-ground temperatures of about 450°C. Thermocouples in the canopy recorded mean temperatures of about 600°C.

Table 6.2. Temperatures in 1995 fires at the Aylesbeare mature stand. Values are means ±SE with the range of values in parentheses. Pyrometer data tested with Friedman test (S) and thermocouple data with ANOVA (F). n=4, all 1 df.

Position	Pyrometer			Thermocouple		
	Low Fuel Load Fires	**High Fuel Load Fires**	**S**	**Low Fuel Load Fires**	**High Fuel Load Fires**	**F**
Soil Surface	23.9 ± 4.0 (5 - 62)	80.6 ± 29.7 (5 - 246)	4.00*	15.24 ± 8.48 (2.62 - 40.20)	16.38 ± 5.63 (7.13 - 31.50)	0.01 NS
Litter Surface	295.0 ± 140 (5 - 704)	220.0 ± 127.0 (38 - 1038)	1.00 NS	-	-	-
Above-ground	433.9 ± 89.3 (101 - 343)	469.0 ±129.0 (101 - 1038)	1.00 NS	632.8 ± 43.0 (511.0 - 698.4)	604.1 ± 34.5 (514.0 - 668.0)	0.24 NS

6.3.2. Microclimate

Mean, minimum and maximum daily values of temperature and relative humidity were extracted from the output of the loggers. The two monitoring positions are plotted on the same graphs and treated as continuous measurements in the analyses.

For clarity, and to smooth daily fluctuations, the means of the mean, minimum and maximum daily temperatures and relative humidities were calculated over 15 day periods. These data are presented in Figures 6.2 and 6.3. The two plots showed similar trends over time, but the differences in the maximum temperatures and minimum and mean relative humidities were more pronounced in the low fuel load fire plot than in the high fuel load fire plot. This may have been because the resprouts were taller and / or denser in one or both of the monitoring positions in this plot.

The overall trends in all variables were similar between the bare ground and resprout covered quadrats in both plots. Mean daily temperatures were nearly identical in the autumn and winter, but began to diverge in the spring (Fig. 6.2). In mid-summer the mean temperatures on bare ground were more than 3°C higher than those under resprouts in the low fuel load fire plot. There was an overall difference in this variable between the two micro-environments (Table 6.3).

Fig 6.2. Annual variation in daily mean, minimum and maximum temperature on bare ground and beneath resprouting *Calluna* in two plots at the Arne mature stand. Data are plotted as mean values over fifteen day intervals.

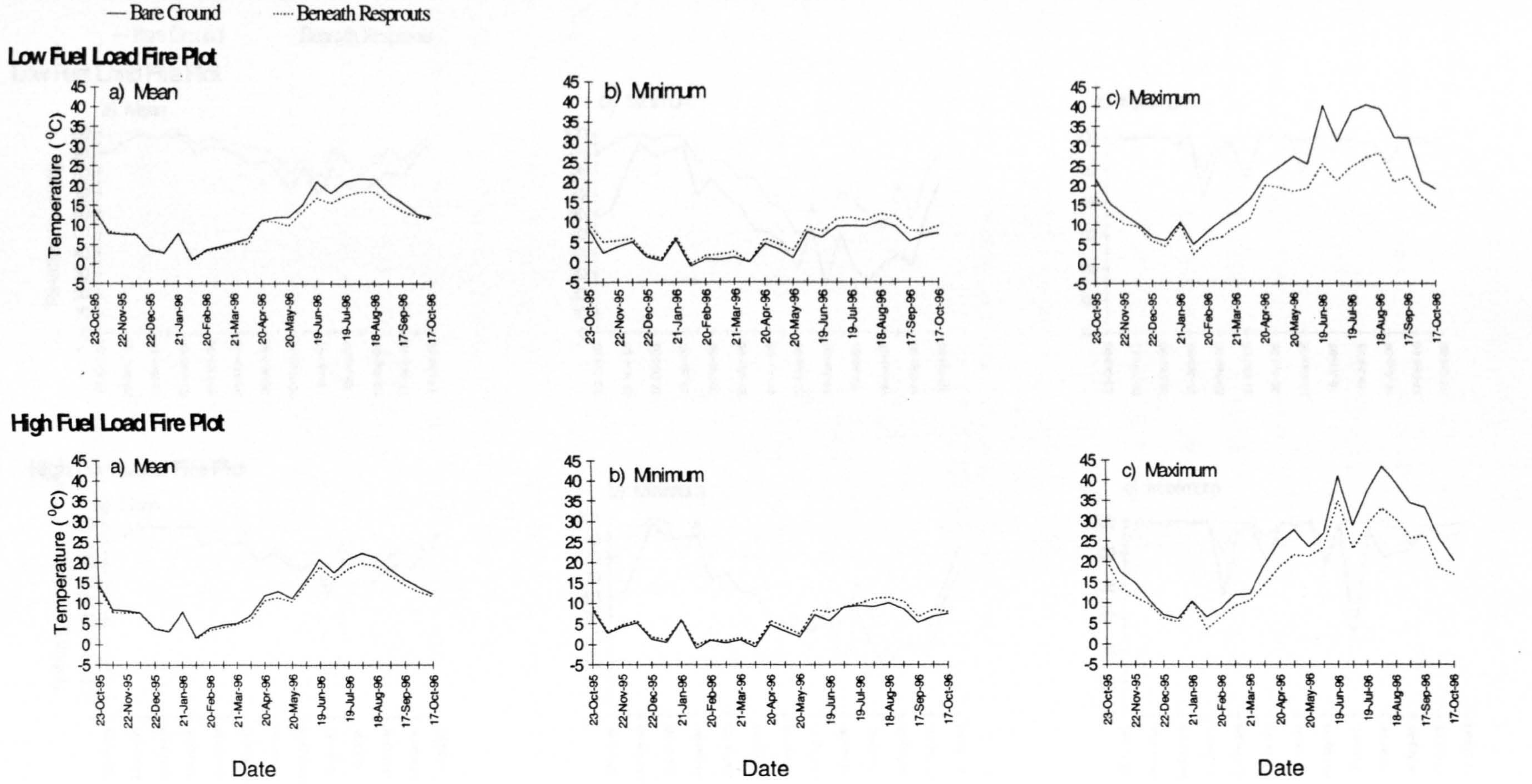
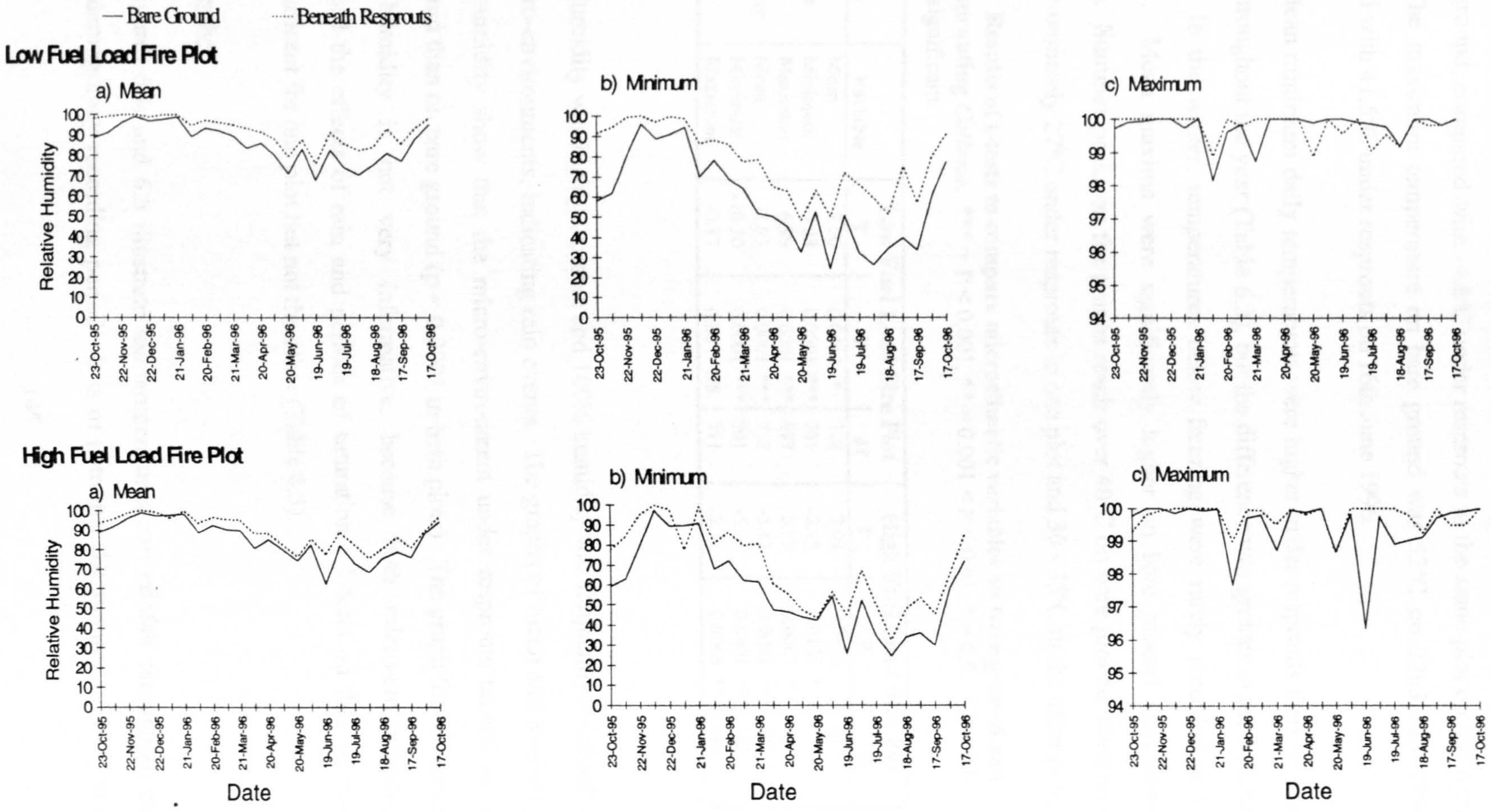


Fig 6.3. Annual variation in daily mean, minimum and maximum relative humidity on bare ground and beneath resprouting *Calluna* in two plots at the Arne mature stand. Data are plotted as mean values over fifteen day intervals.



The lowest temperature recorded in the whole monitoring period was -7.2°C on bare ground, compared with -4.8°C under resprouts in the same plot on 4th April 1996. The maximum temperature on bare ground was 52°C on 22nd July 1996 compared with 41.5°C under resprouts on 16th June 1996.

Mean minimum daily temperatures were higher under resprouts than on bare ground throughout the year (Table 6.3), but the difference was greater in the summer months. In the winter, temperatures below freezing were rarely recorded under resprouts. Mean maxima were significantly higher on bare ground than under resprouts. Summer peaks on the graphs reach over 40°C on bare ground, compared with approximately 27°C under resprouts in one plot and 30 - 35°C in the other plot.

Table 6.3 Results of t-tests to compare microclimatic variables on bare ground and under resprouting *Calluna*. *** = $P < 0.001$, ** = $0.001 < P < 0.01$, * = $0.01 < P < 0.05$, NS = not significant.

		Low Fuel Load Fire Plot			High Fuel Load Fire Plot		
	Variable	**T**	**P**	**df**	**T**	**P**	**df**
Daily Temperature	Mean	2.00	0.0460 *	748	2.03	0.0430 *	739
	Minimum	-3.98	0.0001 ***	701	-2.45	0.0150 *	747
	Maximum	6.99	0.0001 ***	697	5.29	0.0001 ***	705
Daily Relative Humidity	Mean	-7.93	0.0001 ***	712	-5.47	0.0001 ***	706
	Minimum	-10.20	0.0001 ***	701	-5.61	0.0001 ***	743
	Maximum	-0.17	0.86 NS	711	-2.71	0.0068 **	644

Humidity was highly variable and 100% humidity was frequently recorded in both micro-environments, indicating rain events. The graphs of mean and minimum relative humidity show that the micro-environment under resprouts tended to be more humid than on bare ground (p = 0.0001 in both plots). The graph for maximum relative humidity is not very informative, because both micro-environments experienced the effects of rain and periods of saturation. T-tests on this variable were significant for one plot but not the other (Table 6.3).

6.3.4. Weather

Figures 6.4. and 6.5 illustrate the temperatures and rainfall throughout the seedling demography recording period. It is of note that the summer of 1995 was

Figure 6.4. Rainfall and mean daily temperatures recorded at Swanage (16 km from Arne) throughout the seedling demography monitoring period. Temperature data are means and rainfall is the total fallen in each 15 day period

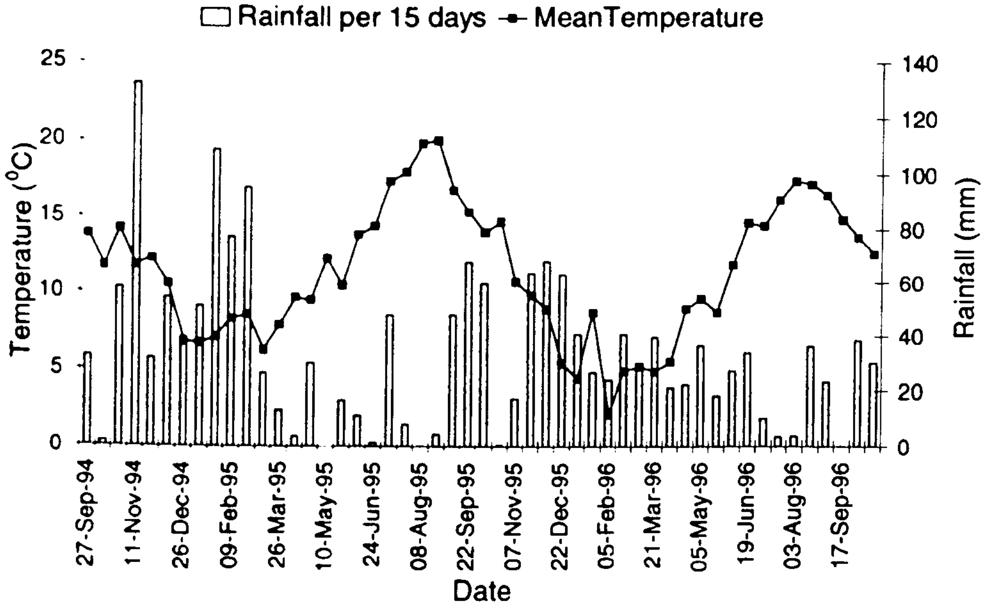
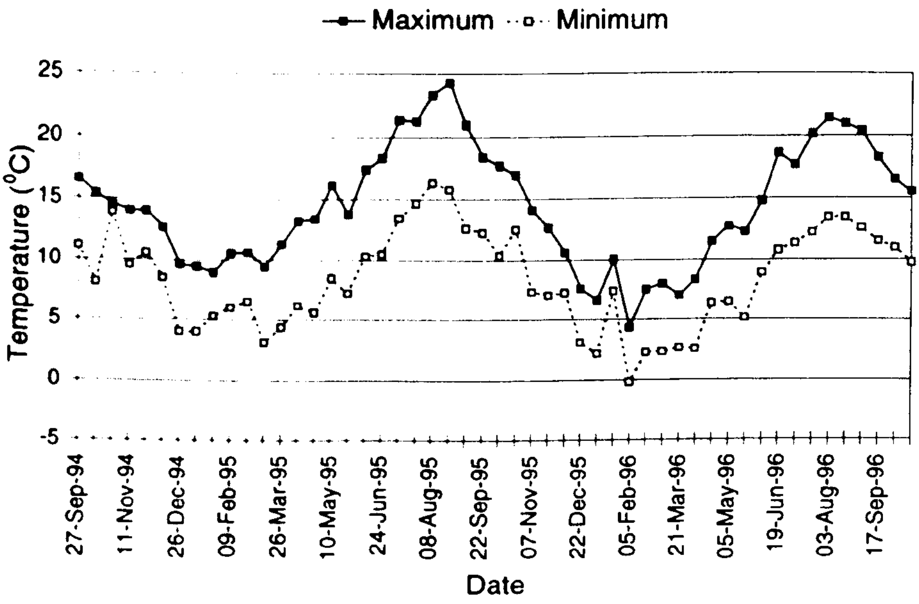


Figure 6.5. Minimum and maximum daily temperatures recorded at Swanage throughout the monitoring period. Data are means over each 15 day period.



hotter and drier than summer 1996. The mean temperature was above 10°C from early May in 1995, compared with mid-June in 1996. There was more rainfall in summer 1996 and it was more evenly distributed.

6.3.5. Seedling Demography

Experiment 1. 1994 Fires

Changes in vegetation cover in mature stands

The definitions of low and high resprout cover at the mature stands were < 10% cover and 40 - 70% cover respectively for the low cover and high cover categories. Vegetation was not maintained at these levels throughout the experiment, so the cover increased in both categories at both stands. The low resprout cover category at Aylesbeare had a higher mean starting resprout cover (2.74% at Arne, 8.55% at Aylesbeare), which increased to a higher level than it did at Arne (Table 6.3). The high cover quadrats at both sites both had an initial mean of about 50% cover , but by February 1996 cover was greater at Arne (77.84%) than it was at Aylesbeare (63.85%).

Table 6.4. Change in vegetation percentage cover in quadrats at mature stands. Values are means (± 1 SE). F = result of one-way ANOVA on the two data sets (n = 6 at each site, 11 df).

Census	Low Cover Category			High Cover Category		
	Arne	Aylesbeare	F	Arne	Aylesbeare	F
Feb 95 (1)	2.74 ± 0.75	8.55 ± 1.30	14.92 **	51.50 ± 0.94	51.82 ± 0.94	0.02 NS
Apr 95 (2)	2.74 ± 0.75	8.55 ± 1.30	14.92 **	51.50 ± 0.94	52.38 ± 0.94	0.13 NS
Jul 95 (3)	6.55 ± 2.21	13.24 ± 2.16	4.69 NS	72.08 ± 2.65	63.15 ± 2.65	5.39 *
Oct 95 (4)	6.80 ± 2.15	13.57 ± 2.04	5.21 *	72.84 ± 3.59	63.43 ± 2.84	4.23 NS
Dec 95 (5)	6.88 ± 2.16	13.57 ± 2.04	5.08 *	73.18 ± 3.48	63.43 ± 2.84	4.71 NS
Feb 96 (6)	6.88 ± 2.16	13.57 ± 2.04	5.08 *	73.73 ± 3.30	63.43 ± 2.84	5.60 *
Apr 96 (7)	6.88 ± 2.16	13.57 ± 2.04	5.08 *	73.73 ± 3.30	63.43 ± 2.84	5.60 *
Aug 96 (8)	6.95 ± 2.15	18.74 ± 2.05	15.73 **	77.84 ± 3.62	63.85 ± 3.06	8.72 *

Survivorship Curves

Figures 6.6 and 6.7 show the survivorship curves of cohorts one to six in the two stands at Arne and Aylesbeare. The initial number of seedlings in each cohort were standardised to 1000 to allow visual comparison of the curves. The first cohort consisted of seedlings present at the first census in February 1995 and subsequent cohorts represented seedlings that had emerged between censuses. Cohorts three (July 1995) and seven (April 1996) are not illustrated because so few seedlings had germinated (Table 6.5). Most seedlings persisted for several months as two cotyledons and approximately 75% died before they could be identified to species, so the ericaceous species have been pooled. None of the seedlings flowered during the monitoring period and very few developed lateral shoots. Almost all the seedlings that survived to be identified at Arne were *Calluna* (> 99%). At both stands at Aylesbeare about 40% of the seedlings that were identified were *Erica cinerea*. There were no *Erica tetralix* seedlings at the degenerate stand at this site and this species represented only 2.6% of identified seedlings at the mature stand. The remaining seedlings in the Aylesbeare stands were *Calluna*.

All stands showed broadly similar trends. Mortality of all cohorts peaked in the first summer after germination. The first two cohorts suffered the highest mortality but the survivorship of the seedlings that survived the first summer was higher in the second summer (curves became less steep). Mortality was noticeably lower for these two cohorts at the Aylesbeare mature stand than at the other stands (Fig. 6.3). The mortality of the autumn cohorts (four and five) was relatively low soon after germination, but the survivorship curves declined more steeply in the summer months. Apart from the Aylesbeare degenerate stand, the mortality of the later cohorts (four - six) in their first summer (1996) was not as high as that of the first two cohorts in summer 1995. The first two cohorts at both stands at Arne seemed to suffer higher mortality than the corresponding stands at Aylesbeare, but there is no obvious difference between the later cohorts.

Table 6.5. The initial number of seedlings in each cohort in each treatment. LF = low fuel load fires, HF = high fuel load fires, LC = low resprout cover, HC = high resprout cover, Con = Controls. Figures in italics indicate the subset of seedlings censused at the mature stands after exclusion of seedlings unaffected by resprouts in high resprout cover categories and seedlings affected by resprouts in low cover quadrats (see text for definition of these subsets).

Stand	**Arne Mature**					**Arne Degenerate**			**Aylesbeare Mature**					**Aylesbeare Degenerate**		
Cohort	LFLC	LFHC	HFLC	HFHC	Con	LF	HF	Con	LFLC	LFHC	HFLC	HFHC	Con	LF	HF	Con
Feb 95 (1)	1714 *1662*	1227 *788*	1110 *1090*	945 *628*	0	637	850	0	925 *821*	696 *495*	674 *589*	641 *534*	0	720	824	38
Apr 95 (2)	185 *179*	219 *156*	88 *88*	88 *55*	0	122	163	2	105 *93*	77 *49*	107 *90*	98 *81*	0	89	87	3
July 95 (3)	21 *21*	22 *21*	3 *3*	15 *15*	0	16	12	0	25 *21*	16 *13*	12 *11*	24 *24*	0	6	9	0
Oct 95 (4)	1329 *1296*	652 *417*	852 *806*	633 *434*	6	404	503	1	1127 *1037*	286 *175*	961 *843*	303 *223*	10	955	1610	80
Dec 95 (5)	326 *320*	159 *118*	227 *218*	71 *63*	3	496	960	35	294 *262*	103 *61*	232 *194*	120 *106*	21	261	455	26
Feb 96 (6)	109 *108*	30 *30*	75 *75*	25 *25*	0	40	84	5	34 *33*	23 *19*	57 *51*	31 *31*	4	11	32	1
Apr 96 (7)	90 *89*	45 *45*	39 *39*	29 *29*	1	11	13	3	22 *21*	7 *5*	0 *0*	12 *10*	0	4	15	0
Aug 96 (8)	11 *11*	2 *2*	6 *6*	6 *6*	0	2	1	0	0 *0*	3 *3*	0 *0*	2 *2*	0	0	1	0

Figure 6.6. Survivorship curves of ericaceous seedlings germinating after 1994 fires at Arne

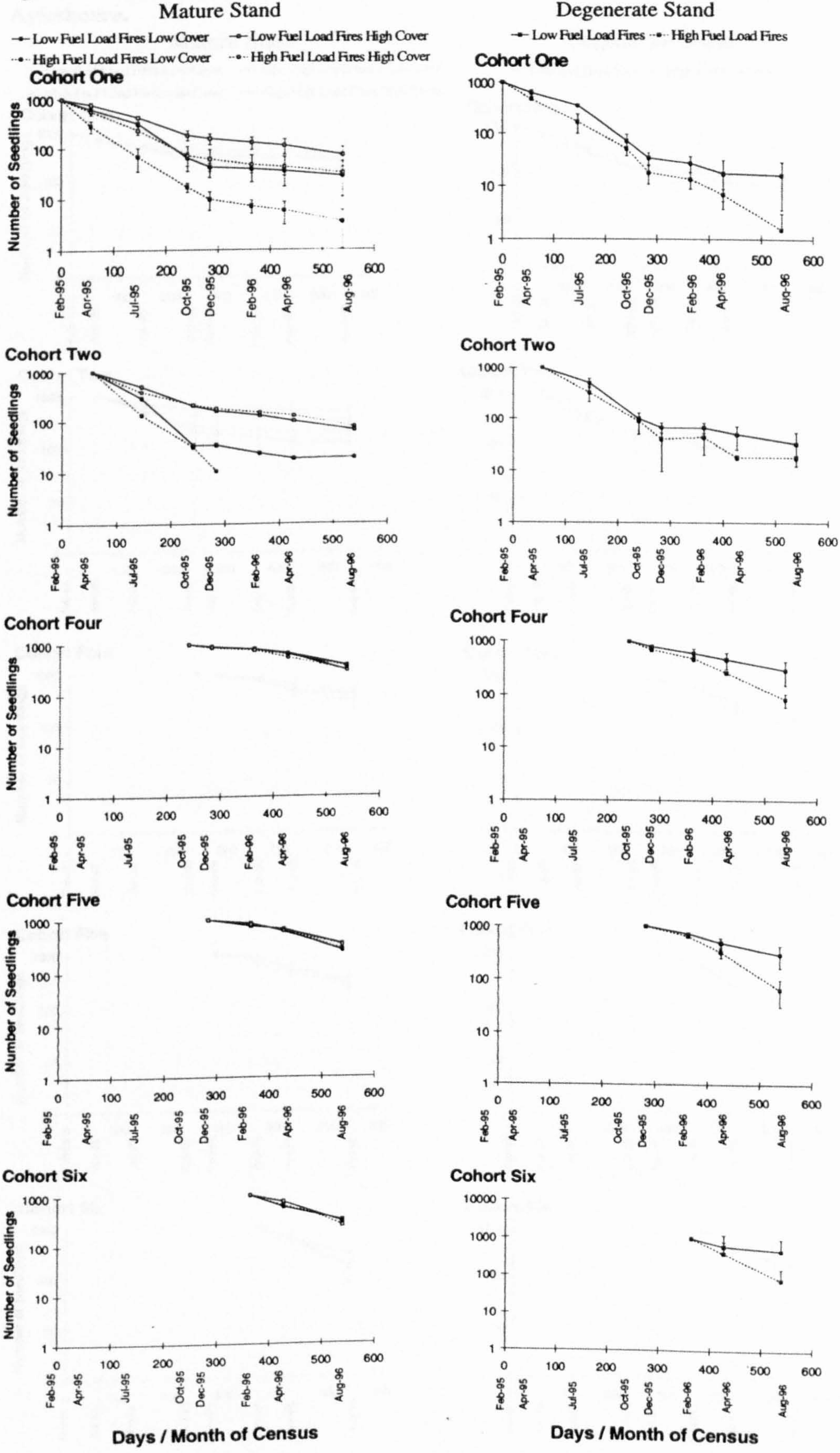
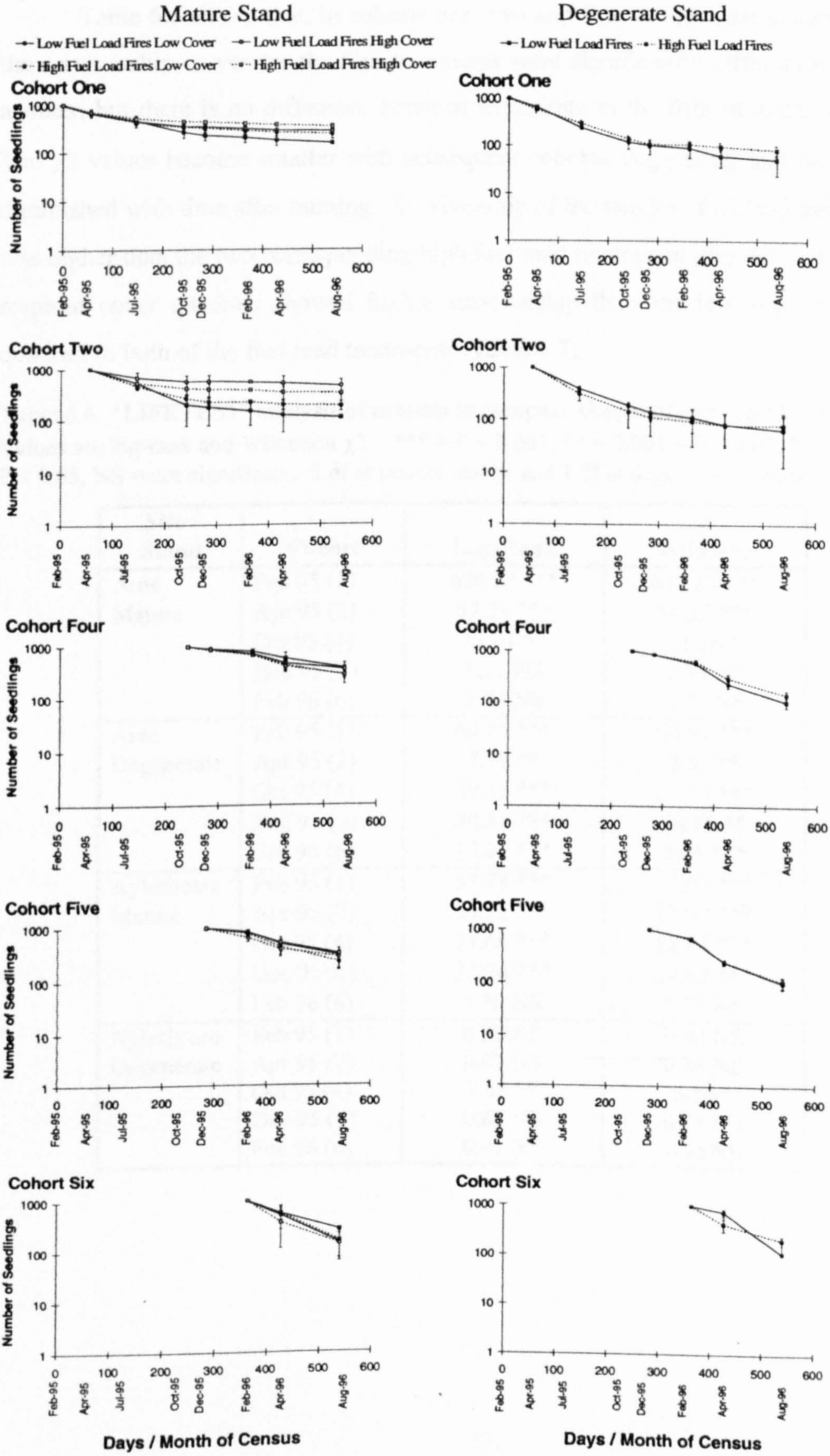


Figure 6.7. Survivorship curves of ericaceous seedlings emerging after 1994 fires at Aylesbeare.



The Arne mature stand

Table 6.6 shows that, in cohorts one, two and four at the Arne mature stand, the survivorship curves for the four treatments were significantly different from one another, but there is no difference between treatments in the fifth of sixth cohorts. The $\chi2$ values become smaller with subsequent cohorts, suggesting that the effects diminished with time after burning. Survivorship of the two low fuel load treatments was higher than the two corresponding high fuel load treatments (Fig. 6.6). The high resprout cover quadrats showed higher survivorship than the low resprout cover quadrats in both of the fuel load treatments (Table 6.7).

Table 6.6. 'LIFETEST' analysis of cohorts to compare shapes of survivorship curves. Values are log-rank and Wilcoxon $\chi2$. *** = $P < 0.001$, ** = $0.001 < P < 0.01$, * = $0.01 < P < 0.05$, NS = not significant. 3 df at mature stands and 1 df at degenerate stands

Site / Stand	Cohort	Log-Rank	Wilcoxon
Arne Mature	Feb 95 (1)	630.23 ***	667.23 ***
	Apr 95 (2)	57.28 ***	54.35 ***
	Oct 95 (4)	12.41 **	11.26 *
	Dec 95 (5)	3.21 NS	2.83 NS
	Feb 96 (6)	2.24 NS	2.97 NS
Arne Degenerate	Feb 95 (1)	60.15 ***	60.91 ***
	Apr 95 (2)	7.79 **	8.65 **
	Oct 95 (4)	39.39 ***	27.30 ***
	Dec 95 (5)	50.56 ***	26.25 **
	Feb 96 (6)	15.51 ***	8.60 ***
Aylesbeare Mature	Feb 95 (1)	37.78 ***	17.05 ***
	Apr 95 (2)	24.52 ***	17.92 ***
	Oct 95 (4)	77.66 ***	88.03 ***
	Dec 95 (5)	21.74 ***	24.67 ***
	Feb 96 (6)	1.59 NS	2.28 NS
Aylesbeare Degenerate	Feb 95 (1)	0.92 NS	0.04 NS
	Apr 95 (2)	0.02 NS	0.34 NS
	Oct 95 (4)	7.58 **	5.74 *
	Dec 95 (5)	0.65 NS	0.88 NS
	Feb 96 (6)	0.01 NS	0.35NS

Table 6.7. Multiple comparisons of cohorts at the Arne mature stand. Values are z-scores calculated from rank statistics and covariance matrices for both log-rank and Wilcoxon statistics. Pairwise comparisons are significant at the 5% level (*) if z > 2.386, which is the adjusted value of z when comparing four populations. LF = Low Fuel, HF = High Fuel, LC = Low Cover, HC = High Cover (of resprouts).

	Cohort One		**Cohort Two**		**Cohort Four**	
Comparison	Log-rank	Wilcoxon	Log-rank	Wilcoxon	Log-rank	Wilcoxon
LFLC LFHC	4.94 *	3.91 *	4.77 *	4.73 *	3.05 *	2.62 *
LFLC HFLC	15.27 *	17.59 *	0.64 NS	1.31 NS	1.52 NS	1.08 NS
LFLC HFHC	2.69 *	5.15 *	3.50 *	2.55 *	0.93 NS	0.38 NS
LFHC HFLC	23.81 *	25.04 *	6.67 *	7.03 *	1.42 NS	1.51 NS
LFHC HFHC	10.54 *	11.09 *	2.62 *	3.64 *	2.81 *	2.94 *
HFLC HFHC	15.05 *	16.11 *	5.05 *	4.81 *	0.96 NS	0.98 NS

The Arne degenerate stand

Seedling survivorship was higher after low fuel load fires than after high fuel load fires in all cohorts (Table 6.6, Fig. 6.6). The values of the log-rank $\chi2$ are larger than the Wilcoxon $\chi2$ in cohorts four, five and six, indicating that survivorship differed more between treatments later in the monitoring period (summer 1996).

The Aylesbeare mature stand

There were treatment differences in all cohorts except cohort six at the Aylesbeare mature stand (Table 6.6, Fig. 6.7). The fourth cohort had the largest $\chi2$ values. More of the pairwise comparisons were significant in cohort four than the other cohorts (Table 6.8). Treatment differences were not as distinct as they were at Arne Mature, with smaller $\chi2$ values, more of which are not significant. There were some significant differences between fuel load treatments and cover categories in the first two cohorts, but there was no consistent pattern. However, survivorship tended to be higher in the high resprout cover categories (Fig. 6.3).

Table 6.8. Multiple comparisons of cohorts at the Aylesbeare mature stand. For legend see Table 6.6.

	Cohort One		Cohort Two		Cohort Four		Cohort Five	
Comparison	Log-rank	Wilcoxon	Log-rank	Wilcoxon	Log-rank	Wilcoxon	Log-rank	Wilcoxon
LFLC LFHC	3.32 •	0.52 NS	4.40 •	3.36 •	7.68 •	8.33 •	1.19 NS	1.50 NS
LFLC HFLC	1.89 NS	0.57 NS	0.58 NS	0.10 NS	6.91 •	7.51 •	2.17 NS	2.40 •
LFLC HFHC	5.84 •	2.95 •	2.27 NS	0.98 NS	8.74 •	9.24 •	3.91 •	4.31 •
LFHC HFLC	1.48 NS	1.22 NS	3.80 •	3.52 •	2.58 •	2.76 •	1.75 NS	1.74 NS
LFHC HFHC	2.99 •	2.77 •	1.96 NS	2.34 NS	2.16 NS	1.96 NS	3.96 •	4.14 •
HFLC HFHC	4.32 •	3.85 •	1.70 NS	1.09 NS	1.09 NS	1.37 NS	1.39 NS	1.57 NS

The Aylesbeare degenerate stand

All cohorts except cohort four showed no significant treatment differences at the Aylesbeare degenerate stand (Table 6.6). Fire temperatures were not significantly different between fuel load treatments at this stand (Table 6.1), so a treatment effect was not expected. The significant difference evident in cohort four is probably a random effect.

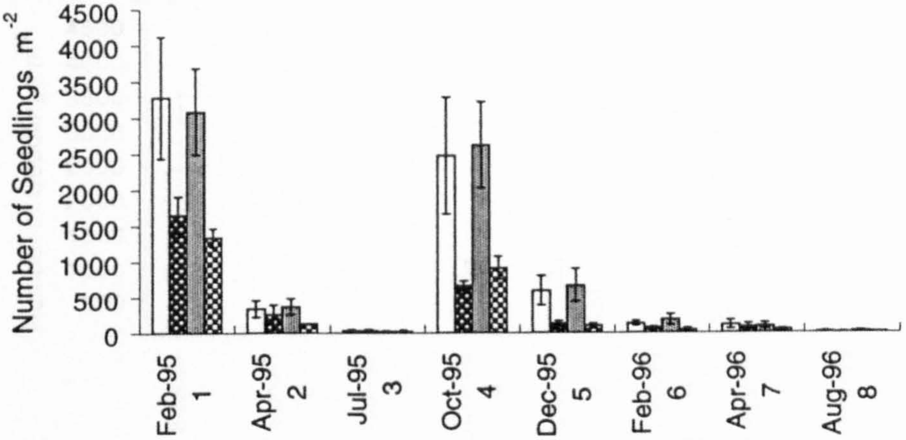
Population Flux

Patterns in overall seedling density, emergence and death over time are shown in Figures 6.8 - 6.11. Control plots are not illustrated on the graphs or included in the analyses because few seedlings germinated under the canopy (Table 6.5). Tables 6.9. - 6.11 are results of repeated measures ANOVA on these variables and on proportional mortality. ANOVAs on individual censuses are in Appendix Three. There is no table for individual censuses at the degenerate stands, because no significant differences were found for any of the variables.

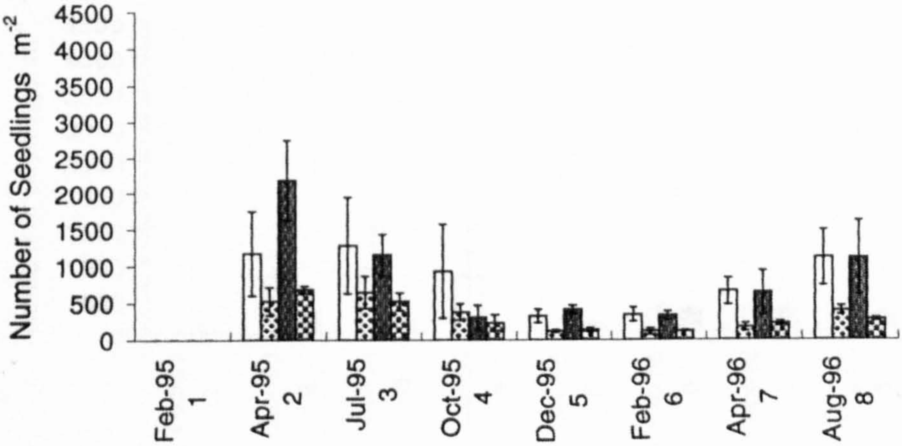
Fig. 6.8. Population flux at the Arne mature stand. Data are means ± 1 SE (n=3)

□ Low Fuel Load Fires Low Cover
▦ High Fuel Load Fires Low Cover
▩ Low Fuel Load Fires High Cover
▨ High Fuel Load Fires High Cover

a) Emergence



b) Deaths



c) Density

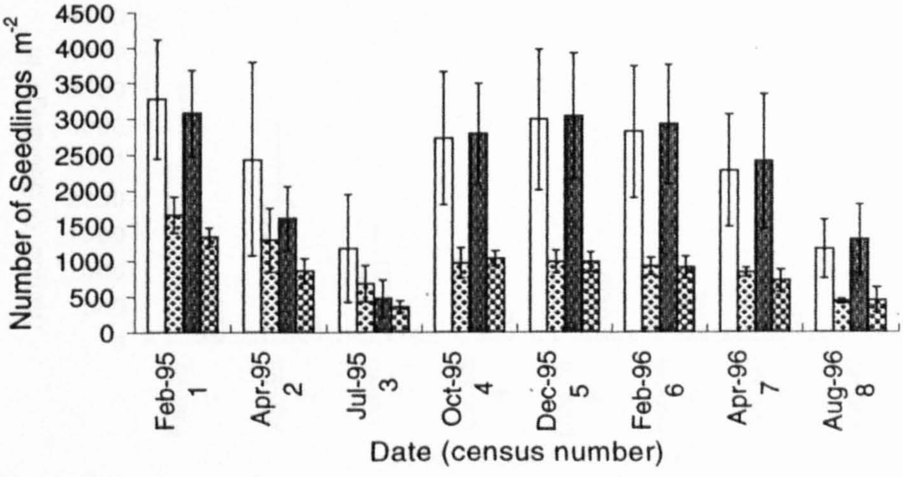
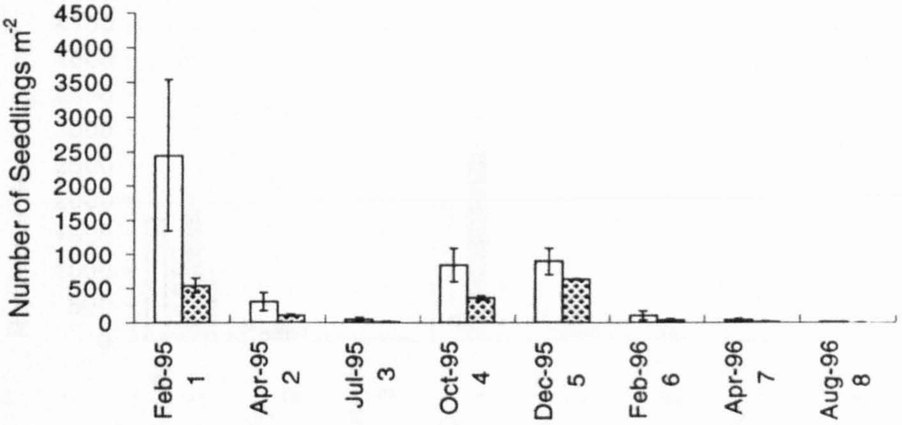


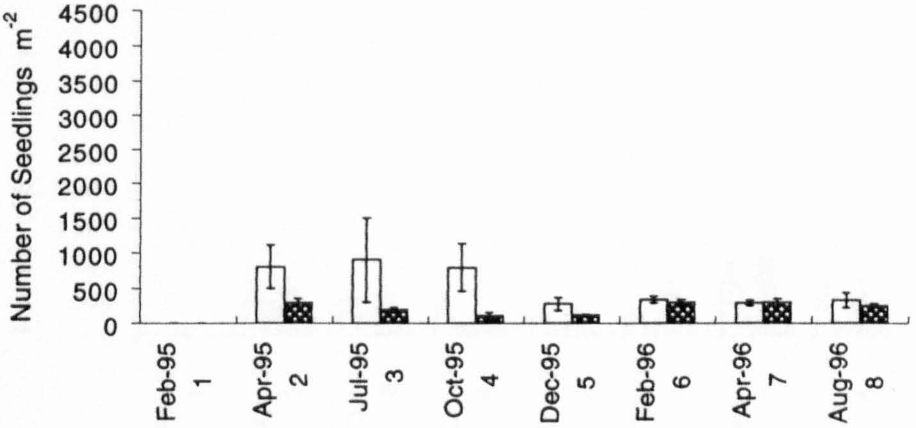
Fig. 6.9. Population flux at the Arne degenerate stand.
Data are means ± 1 SE (n=3)

☐ Low Fuel Load Fires ▨ High Fuel Load Fires

a) Emergence



b) Deaths



c) Density

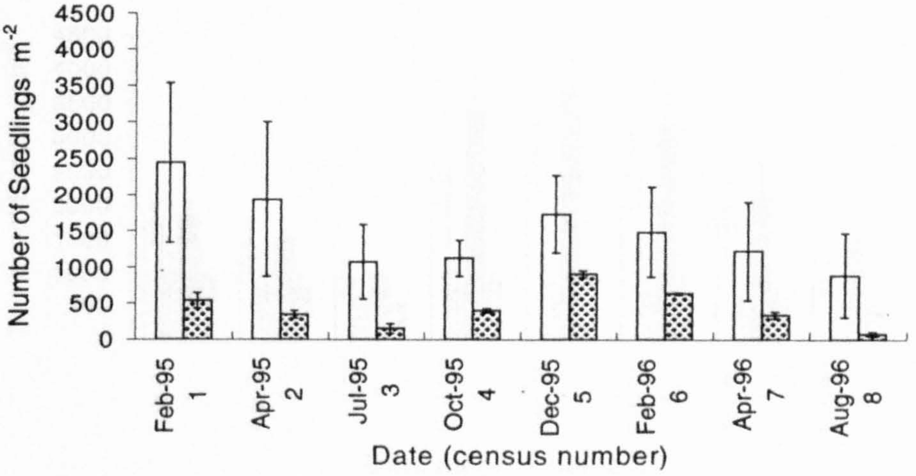
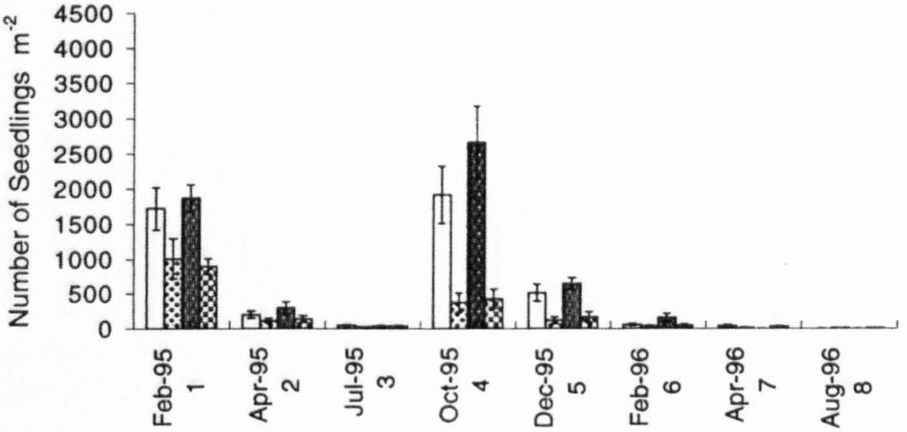


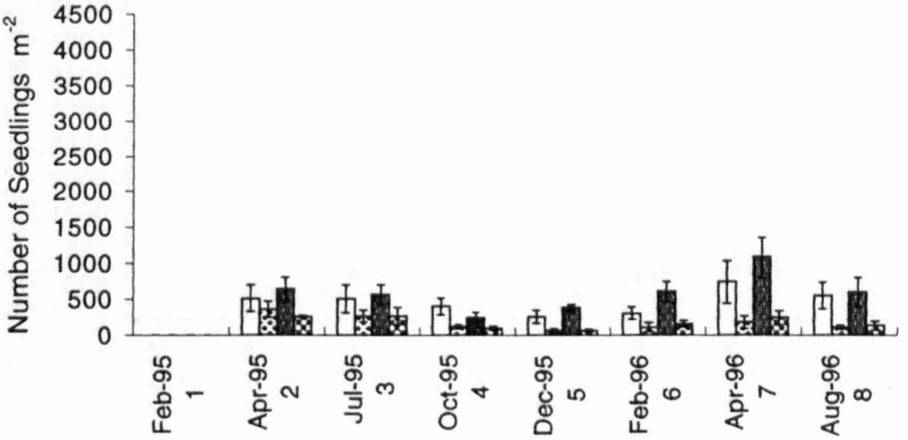
Fig. 6.10. Population flux at the Aylesbeare mature stand. Data are means ± 1 SE (n=3)

☐ Low Fuel Load Fires Low Cover ▨ Low Fuel Load Fires High Cover
■ High Fuel Load Fires Low Cover ▩ High Fuel Load Fires High Cover

a) Emergence



b) Deaths



c) Density

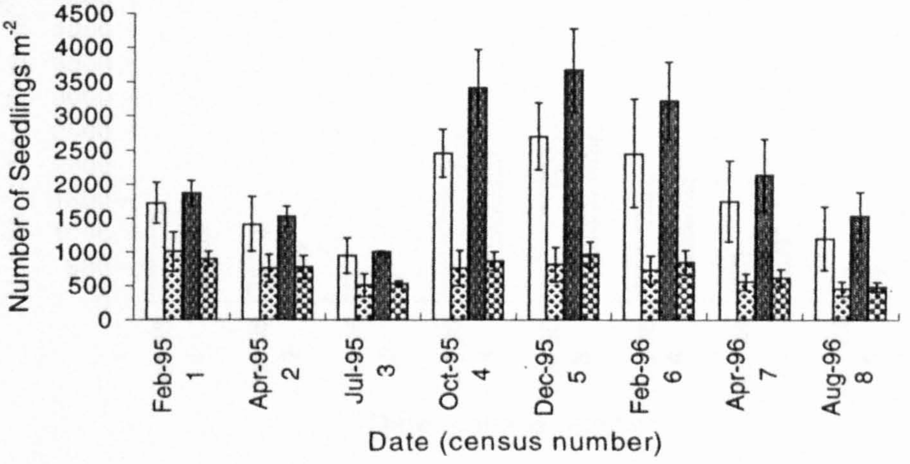
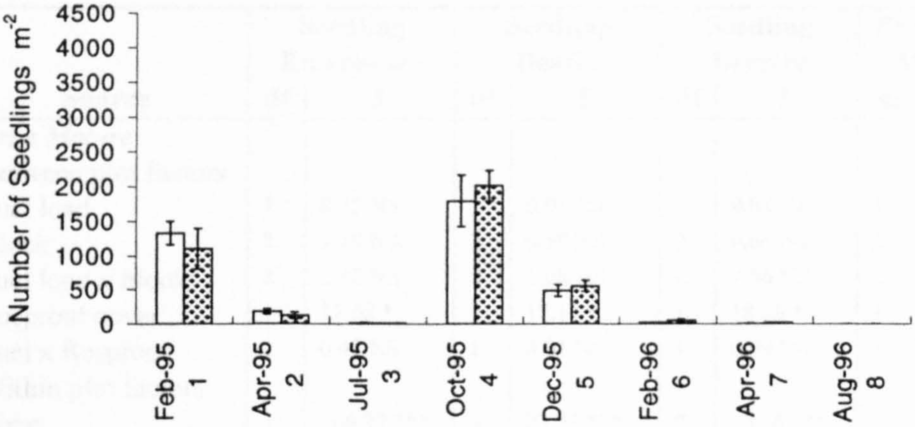


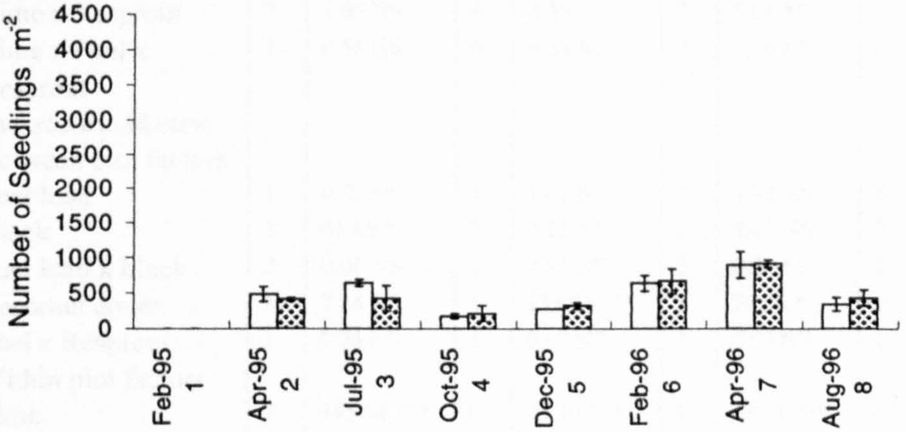
Fig. 6.11. Population flux at the Aylesbeare degenerate stand.
Data are means ± 1 SE (n=3)

□Low Fuel Load Fires ▨High Fuel Load Fires

a) Emergence



b) Deaths



c) Density

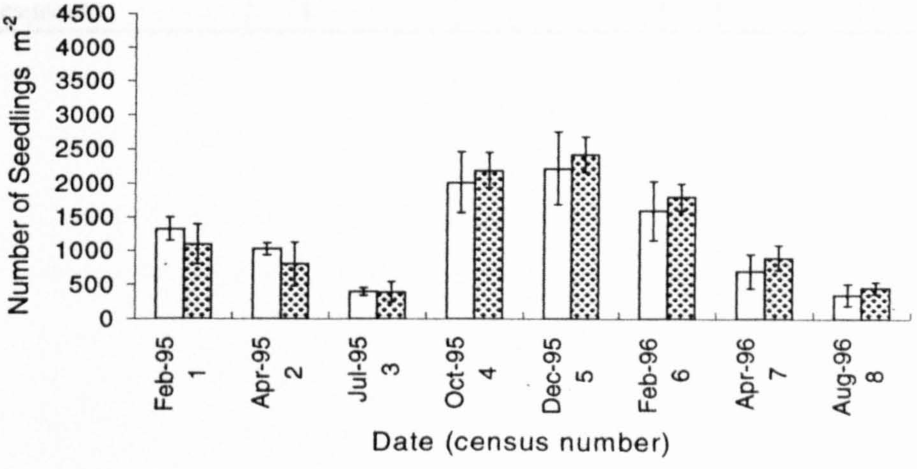


Table 6.9. Repeated Measures ANOVA on the effects of burning different fuel loads on seedling emergence, death, density and proportional mortality at the mature stands. Huynh-Feldt adjustment was applied to probability values of within-plot factors. MS fuel load x block was used as denominator to calculate F-value of fuel load and block and MS time x fuel load x block used to test time, time x fire and time x block. *** = P < 0.001, ** = 0.001 < P < 0.01, * = 0.01 < P < 0.05, NS = not significant.

	Seedling Emergence		Seedling Deaths		Seedling Density		Proportional Mortality	
Source	**df**	**F**	**df**	**F**	**df**	**F**	**df**	**F**
Arne Mature								
Between plot factors								
Fuel load	1	0.35 NS	1	0.01 NS	1	0.08 NS	1	158.29 **
Block	2	1.19 NS	2	0.59 NS	2	0.64 NS	2	52.80 *
Fuel load x block	2	2.12 NS	2	3.08 NS	2	4.56 NS	2	0.03 NS
Resprout cover	1	12.08 *	1	17.11 *	1	18.66 *	1	2.15 NS
Fuel x Resprout	1	0.47 NS	1	0.01 NS	1	0.09 NS	1	0.03 NS
Within plot factors								
Time	7	166.27 ***	6	22.57 ***	7	45.56 ***	6	87.55 ***
Time x Fuel	7	1.17 NS	6	2.58 NS	7	2.52 NS	6	6.67 **
Time x Block	14	4.73 **	12	3.07 *	14	4.11 **	12	5.42 **
Time x Fuel x Block	14	0.49 NS	12	1.31 NS	14	0.94 NS	12	0.50 NS
Time x Resprout	7	1.60 NS	6	2.39 NS	7	5.01 ***	6	0.35 NS
Time x Fuel x Resprout	7	0.56 NS	6	0.58 NS	7	0.16 NS	6	0.41 NS
Aylesbeare Mature								
Between plot factors								
Fuel load	1	0.02 NS	1	1.01 NS	1	3.32 NS	1	0.12 NS
Block	2	61.85 *	2	2.13 NS	2	0.62 NS	2	2.40 NS
Fuel load x block	2	0.06 NS	2	2.81 NS	2	0.22 NS	2	0.64 NS
Resprout cover	1	7.28 NS	1	133.95 ***	1	20.56 *	1	2.30 NS
Fuel x Resprout	1	0.26 NS	1	0.69 NS	1	0.09 NS	1	0.00 NS
Within plot factors								
Time	7	495.94 ***	6	43.40 ***	7	59.51 ***	6	97.94 ***
Time x Fuel	7	7.41 ***	6	6.56 **	7	0.96 NS	6	8.09 **
Time x Block	14	11.47 ***	12	26.29 ***	14	16.03 ***	12	21.40 ***
Time x Fuel x Block	14	0.46 NS	12	0.44 NS	14	0.68 NS	12	0.35 NS
Time x Resprout	7	10.13 ***	6	5.64 **	7	9.28 ***	6	2.72 *
Time x Fuel x Resprout	7	4.68 **	6	0.44 NS	7	0.25 NS	6	0.81 NS

Table 6.10. Repeated Measures ANOVA on the effects of burning different fuel loads on seedling emergence, death , density and proportional mortlaity at the degenerate stands. Huynh-Feldt adjustment was applied to probability values of time, time x fuel load and time x block.

	Seedling Emergence		**Seedling Deaths**		**Seedling Density**		**Proportional Mortality**	
Source	**df**	**F**	**df**	**F**	**df**	**F**	**df**	**F**
Arne Degenerate								
Fuel load	1	2.00 NS	1	2.28 NS	1	3.14 NS	1	5.28 NS
Block	2	0.16 NS	2	0.20 NS	2	0.50 NS	2	2.09 NS
Time	7	121.08 ***	6	1.28 NS	7	13.05 ***	6	11.83 ***
Time x Fuel	7	1.15 NS	6	2.02 NS	7	2.26 NS	6	3.30 *
Time x Block	14	2.59 *	12	0.84 NS	14	1.33 NS	12	3.08 *
Aylesbeare Degenerate								
Fuel load	1	2.08 NS	1	0.02 NS	1	0.01 NS	1	0.63 NS
Block	2	0.49 NS	2	0.17 NS	2	0.01 NS	2	2.13 NS
Time	7	40.22 ***	6	33.28 ***	7	250.25 ***	6	54.62 ***
Time x Fuel	7	0.37 NS	6	2.09 NS	7	10.15 ***	6	1.44 NS
Time x Block	14	0.26 NS	12	3.79 NS	14	8.27 ***	12	5.41 **

Seedling Emergence

All stands showed peaks in recruitment in October 1995 (Figs 6.8 - 6.11). The initial peak in February 1995 represented germination and mortality over a longer period (October 1994 - February 1995). There was negligible seedling emergence in the summer censuses of July 1995 and August 1996. Repeated measures ANOVA showed that this seasonal variation in recruitment was significant for all sites (Tables 6.9 - 6.11). The number of seedlings emerging between July and October 1995 at Arne did not exceed the original number (Figs 6.8 and 6.9). In both stands at Aylesbeare, however, the peaks in emergence at this time were greater than the number of seedlings present at the first census (Figs 6.10 and 6.11).

Table 6.11. Repeated Measures nested ANOVA on seedling emergence, death, density and proportional mortality to compare stands at Arne and Aylesbeare. The high cover quadrats at the mature stands were not used in the analysis. Huynh-Feldt adjustment was applied to probability values of within-plot factors. MS block (stand) was used as denominator to calculate F-value of fuel load. MS time x block (stand) was used to test time x fuel load

	Seedling Emergence		**Seedling Deaths**		**Seedling Density**		**Proportional Mortality**	
Source	**df**	**F**	**df**	**F**	**df**	**F**	**df**	**F**
Arne								
Between plot factors								
Stand	1	7.98 *	1	6.83 NS	1	10.66 *	1	43.23 **
Fuel load	1	1.32 NS	1	1.30 NS	1	2.28 NS	1	1.13 NS
Block (stand)	4	0.46 NS	4	0.92 NS	4	0.69 NS	4	2.47 NS
Stand x Fuel load	1	1.10 NS	1	1.71 NS	1	1.89 NS	1	9.45 *
Within plot factors								
Time	7	160.13 ***	6	6.34 **8	7	31.92 ***	6	37.76 ***
Time x Stand	7	2.30 NS	6	1.10 NS	7	3.27 *	6	0.94 NS
Time x Fuel load	7	0.90 NS	6	2.57 *	7	2.99 *	6	2.98 *
Time x Block (stand)	28	2.86 **	24	1.43 NS	28	2.08 *	24	2.78 **
Time x Stand xFuel	7	0.24 NS	6	1.19 NS	7	1.01 NS	6	3.87 **
Aylesbeare								
Between plot factors								
Stand	1	12.61 *	1	0.60 NS	1	29.84 **	1	9.18 *
Fuel load	1	4.00 NS	1	0.80 NS	1	0.18 NS	1	0.02 NS
Block (stand)	4	1.41 NS	4	0.34 NS	4	0.23 NS	4	1.55 NS
Stand x Fuel load	1	0.35 NS	1	0.36 NS	1	0.38 NS	1	0.23 NS
Within plot factors								
Time	7	143.65 ***	6	36.22 ***	7	162.73 ***	6	56.73 ***
Time x Stand	7	2.44 *	6	0.86 NS	7	1.93 NS	6	0.85 NS
Time x Fuel load	7	3.16 *	6	2.20 NS	7	1.19 NS	6	2.06 NS
Time x Block (stand)	28	0.58 NS	24	6.33 ***	28	6.55 ***	24	3.99 ***
Time x Stand xFuel	7	1.19 NS	6	3.19 *	7	4.76 **	6	1.81 NS

Repeated measures ANOVA showed there was no consistent effect of fuel load on emergence at any of the stands (Tables 6.9 - 6.11). The only differences between fuel load treatments were at censuses three and six at the mature stand at Arne and census seven at the mature stand at Aylesbeare (Appendix Three). So few new seedlings were observed at these censuses (Table 6.5), that this difference was probably due to chance.

Seedling emergence at both the mature stands was significantly different between the resprout cover categories overall (Table 6.9, Figs 6.8 and 6.10) but not at all censuses (Appendix Three). Resprout cover had most effect on density of emergence at the times of peak germination (censuses one, four and five).

Seedling emergence was significantly different between the mature and degenerate stands at both sites (Table 6.11). The low cover quadrats at the mature stands showed more recruitment than the degenerate stands.

Deaths

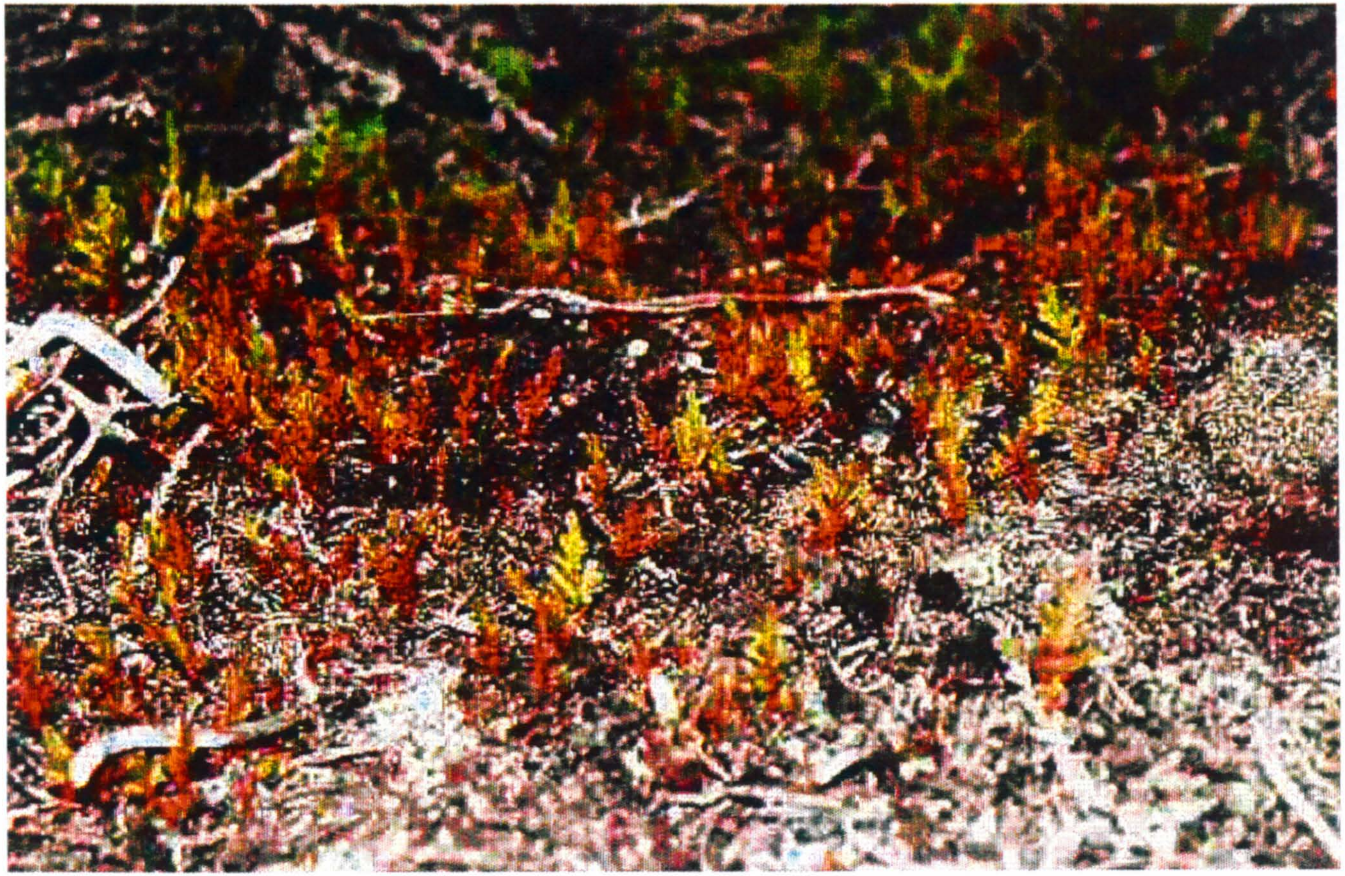
There was significant seasonal variation in the number of deaths m^{-2} at all the stands except the Arne degenerate stand (Tables 6.9 and 6.10). At the Arne mature stand, most deaths occurred early in the monitoring period, when seedling density was highest (Figs 6.8 and 6.9). At Aylesbeare, there were most deaths in February and April 1996, following the peak in emergence of winter 1995 / 96 (Figs 6.6 and 6.7).

There were no differences between the two fuel load treatments at any of the censuses at any of the stands (Tables 6.9 and 6.10, Appendix Three) and no overall difference between stands at either site (Table 6.11). The lack of interaction between time and stand indicates that the pattern of seedling deaths throughout the monitoring period did not differ between stands at either site (Table 6.11). At both the mature stands, the number of seedlings dying m^{-2} was significantly lower in high resprout cover quadrats than in low cover quadrats at most censuses (Appendix Three), due to the lower seedling density (Table 6.9).

Seedling density

Seedling density peaked in the autumn and winter months and was at a minimum in the summer (Figs 6.8 - 6.11). The density at the end of the monitoring period was lower than the starting density at all stands. None of the stands showed significant differences in seedling densities between fuel load treatments (Tables 6.9 - 6.11). Resprout cover had a significant effect on seedling density at both the mature stands (Table 6.9). The mean initial density at the Arne mature stand was about 3000 seedlings m^{-2} in the low cover category compared to about 1500 seedlings m^{-2} in the high cover category (Fig. 6.8). Plate 6.4 illustrates the high density of seedlings in a

Plate 6.4. *Calluna* **seedlings in a low resprout cover quadrat at the Arne mature stand (February 1996)**



low resprout cover quadrat at the Arne mature stand. At the Aylesbeare mature stand the mean initial densities in the low and high resprout cover categories were about 1800 and 1000 seedlings m^{-2} respectively (Fig. 6.10). There was a significant interaction between time and resprout cover at both sites (Table 6.9), because seedling densities in the low cover quadrats fluctuated between wider limits than the densities in the high cover quadrats.

Seedling densities were significantly different between stands at both sites (Table 6.11). Seedling densities at the degenerate stands were lower than the low cover categories at the mature stands (Figs 6.8 - 6.11). The density of seedlings in the low resprout cover quadrats at the Arne mature stand remained between 2500 and 3500 m^{-2} in the autumn and winter months (Fig. 6.8). At the Arne degenerate stand the mean starting density after low fuel load fires was about 2500 seedlings m^{-2} compared to only 500 m^{-2} after high fuel load fires (Fig, 6,9). However, this trend was not significant. At Aylesbeare, the peak in density at the mature stand in winter 1995 was about 3000 seedlings m^{-2} (Fig, 6.9). The initial density at the degenerate stand was about 1200 seedlings m^{-2}, rising to over 2000 m^{-2} in October - December 1995 (Fig. 6.10). The seedling density in the low cover quadrats at the mature stand at Arne was quite stable between October 1995 and February 1996 (Fig. 6.8), whereas the density at the degenerate stand had a distinct peak in December 1995 (Fig 6.9). This caused a significant time x stand interaction at this site (Table 6.11).

Proportional Mortality

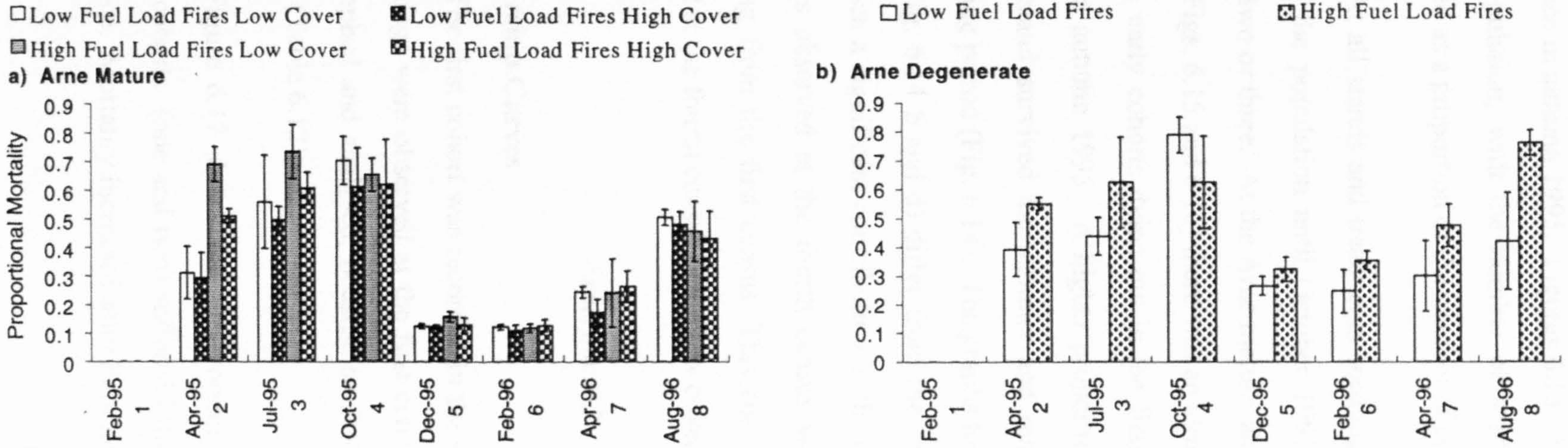
In Figure 6.12, the number of seedlings dying between censuses is expressed as a proportion of the number of seedlings alive at the end of the previous census to illustrate the relative impact of mortality on the populations throughout the recording period. Seasonal variation in mortality at all stands was demonstrated by repeated measures ANOVA (Tables 6.9 - 6.11). There was high mortality in summer 1995, reaching values greater than 70% in both stands at Arne (Fig. 6.12). The proportion dying the following summer at the mature stand at Arne decreased to about 45%, but the mean of both treatments at the degenerate stand was about 60% (Fig. 6.12b). Proportional mortality at the Aylesbeare degenerate stand was about 60% in both summers (Fig. 6.12d). Proportional mortality was lowest at the Aylesbeare mature stand , and about 30 - 40% was lost from the population in both summers (Fig. 6.12c). Winter mortality in 1995 was lower at all stands at 10 - 30%.

There was an overall effect of fuel load at Arne Mature (Table 6.9), but only the second census exhibited a significant difference in the individual ANOVAs (Appendix Three, Fig. 6.12a). At this census, proportional mortality was higher after high fuel load fires than after low fuel load fires. The mature stand at Aylesbeare did not show a similar effect. There were no differences between fuel load treatments at either of the degenerate stands (Table 6.10).

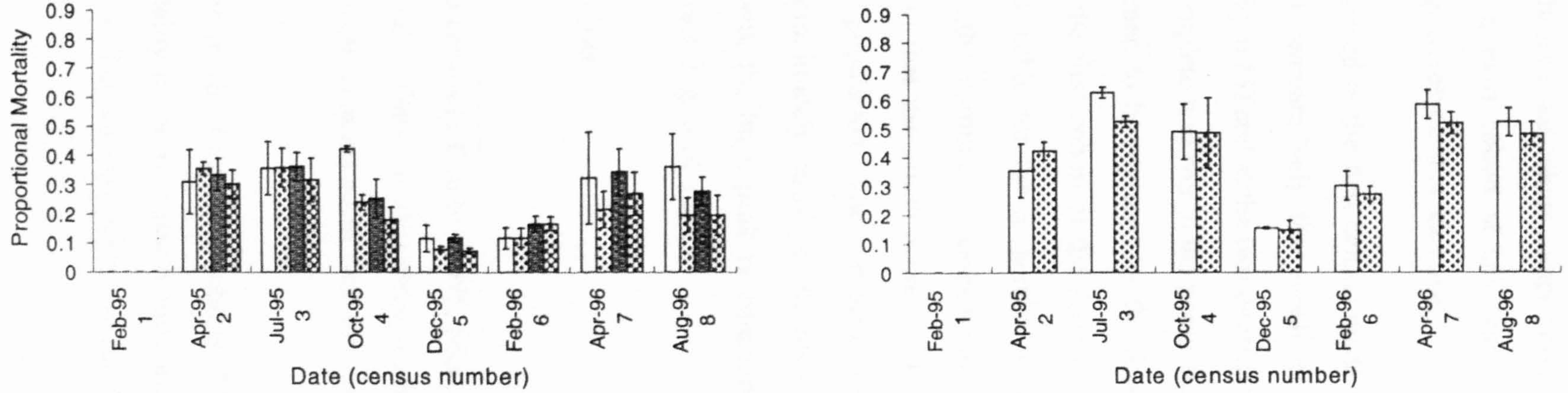
Resprout cover had no overall effect on proportional mortality at the mature stands (Table 6.9). The only significant difference was observed in the fourth census at the Aylesbeare mature stand (Fig. 6.12c, Appendix Three), where mortality in the low fuel / low cover treatment was higher than in the other treatments. This difference may be the main cause of significant time x resprout cover and time x fuel load interactions at this stand (Table 6.9).

Proportional mortality was significantly different between stands at both Arne and Aylesbeare (Table 6.11), and tended to be higher at the degenerate stands than in the low cover quadrats at the mature stands (Fig, 6.12). There was no significant difference between stands at the first four censuses at Arne, but proportional mortality was higher at the degenerate stand in censuses five - eight (Fig. 6.12, Appendix Three). The proportional mortality at Aylesbeare was only significantly different between stands at censuses three, six and eight (Appendix Three).

Fig. 6.12. Proportional Mortality at all stands. Mortality was calculated as the number of seedlings from all cohorts dying at census *t+1* as a proportion of the number alive at census *t*.


a) **Arne Mature**

b) **Arne Degenerate**


c) **Aylesbeare Mature**

d) **Aylesbeare Degenerate**

Relative contribution of the different cohorts to the overall population

The overall population flux described previously, indicates high mortality of the early cohorts in the first summer of germination, followed by a peak in emergence in autumn 1995. Figures 6.13 - 6.16 illustrate the cohort composition of each population, with the number of seedlings in each cohort at any one time expressed as a proportion of the number of seedlings observed at census one.

At all stands and treatments seedlings observed at the first census made up most of the population until October 1995, with comparatively few seedlings in cohorts two or three. At the Arne mature stand (Fig. 6.13) and at the two degenerate stands (Figs. 6.15 and 6.16) there was an almost complete turnover in the population, with the early cohorts dying out in the first summer, to be replaced by the fourth cohort in autumn 1995. A higher proportion of the first cohort at the Aylesbeare mature stand survived the summer and remained stable for the remainder of the monitoring period (Fig. 6.14). The graphs for the high resprout cover category at this stand (Fig. 6.14 b and d) differ from the others, in that the fourth cohort did not make such a significant contribution to the overall population. The number of new seedlings observed at the fourth census was approximately equal to the number remaining from the first census. This contrasts with the huge peak in emergence apparent at the fourth census in the low cover quadrats (Fig. 6.14 a and c).

Experiment 2: 1995 Fires

Survivorship Curves

The first cohort was recorded in the second census in October 1995, because no seedlings were observed at the first census in July. Only the first three cohorts were graphed and analysed, because so few seedlings germinated at censuses four and five (Table 6.12).

Figure 6.17 shows the survivorship curves of the first three cohorts. The autumn cohorts (one and two) suffered little mortality in the first few months after emergence. Mortality increased after February 1996. The survivorship curve for the

Fig. 6.13. Proportional contribution of cohorts to the total population at the Arne mature stand.

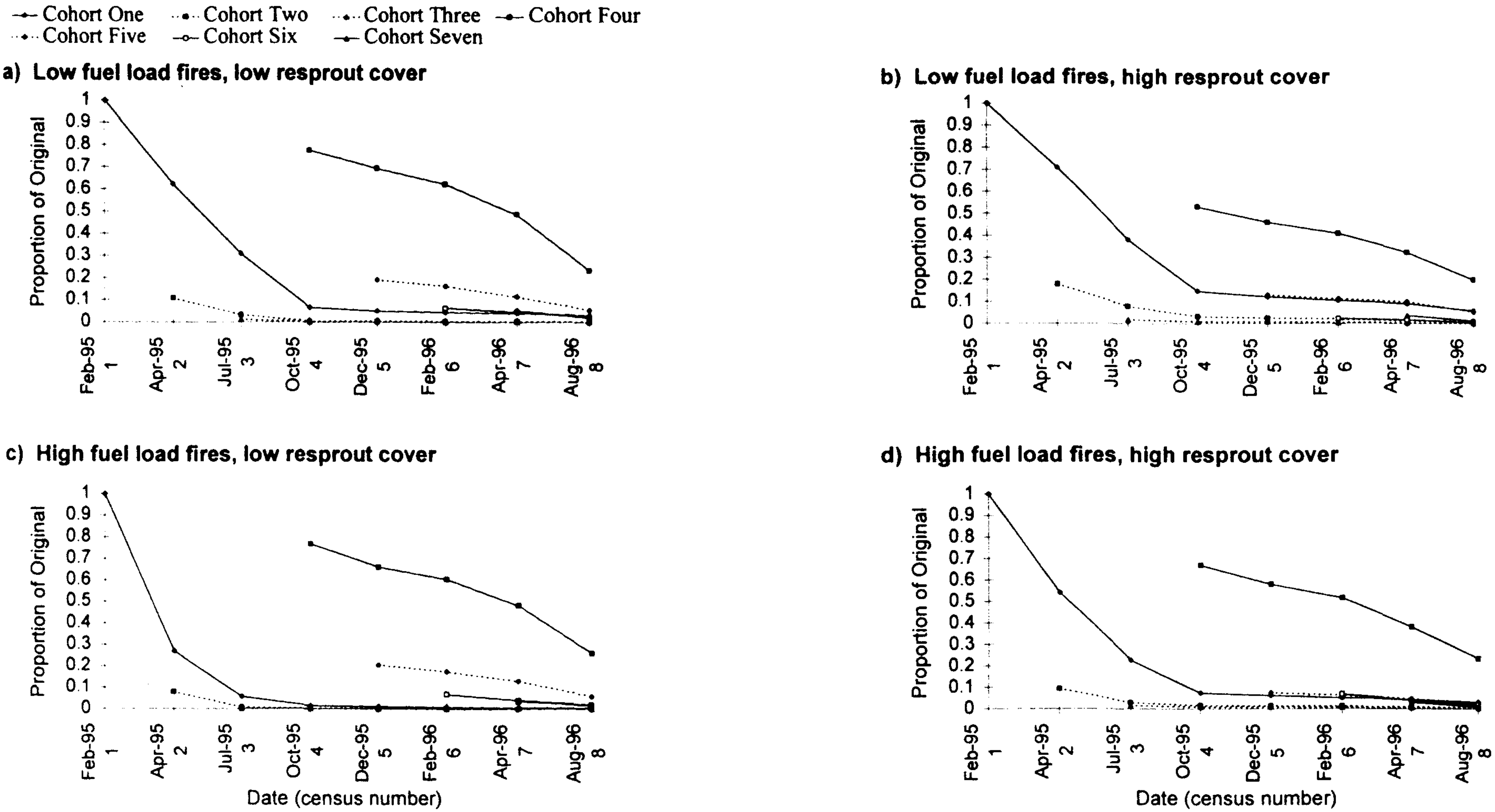
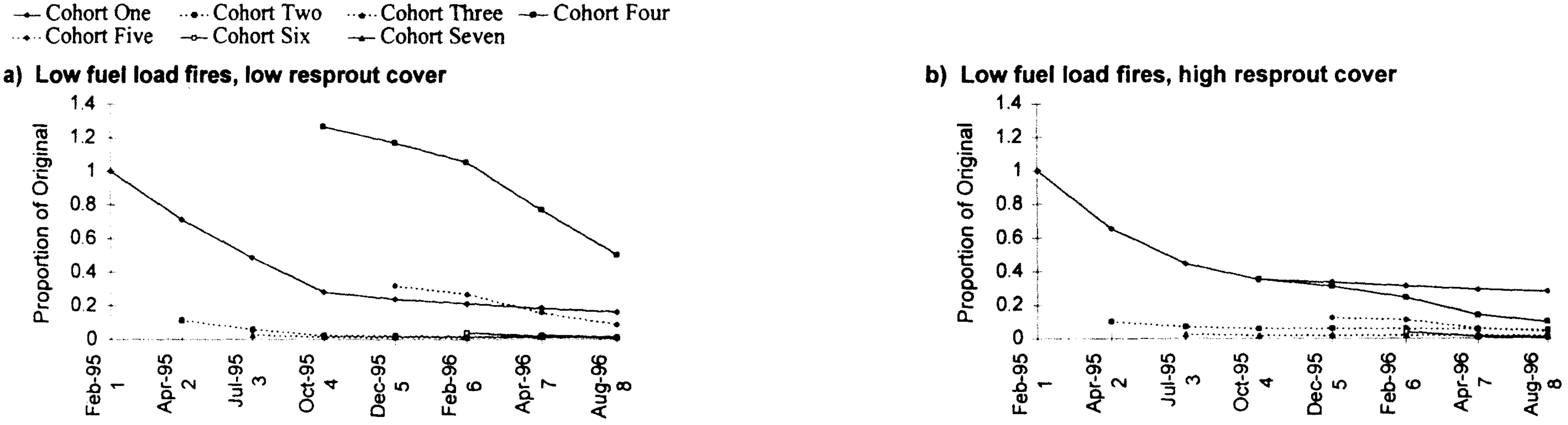


Fig. 6.14. Proportional contribution of cohorts to the total population at the Aylesbeare mature stand



a) Low fuel load fires, low resprout cover

b) Low fuel load fires, high resprout cover

c) High fuel load fires, low resprout cover

d) High fuel load fires, high resprout cover

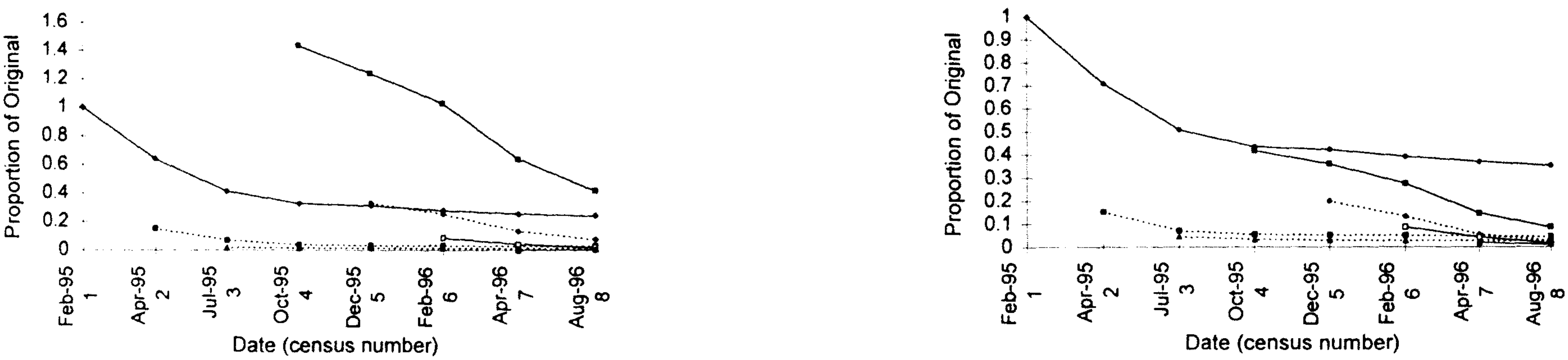
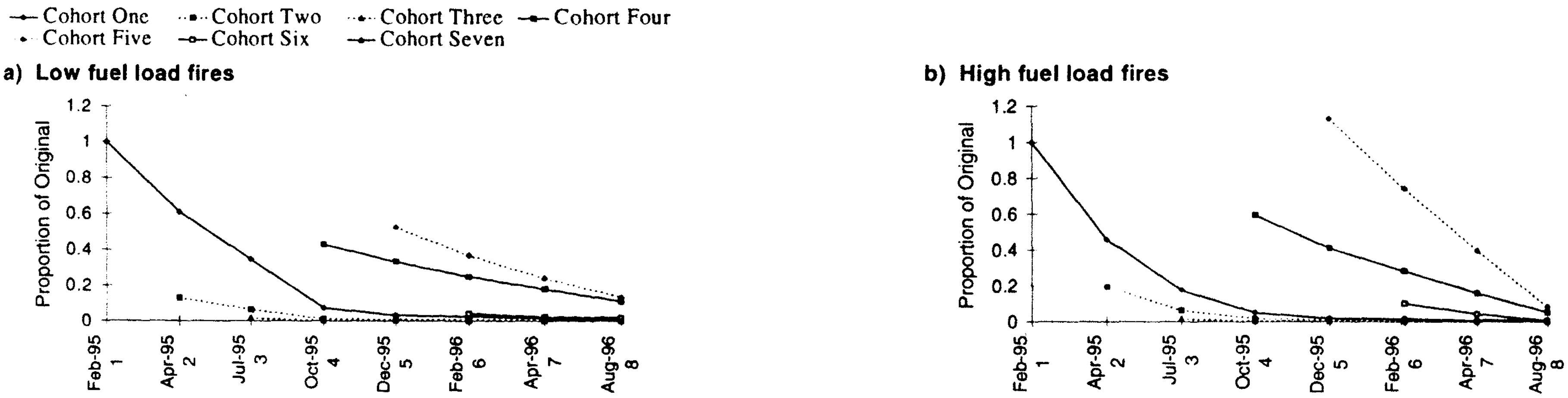
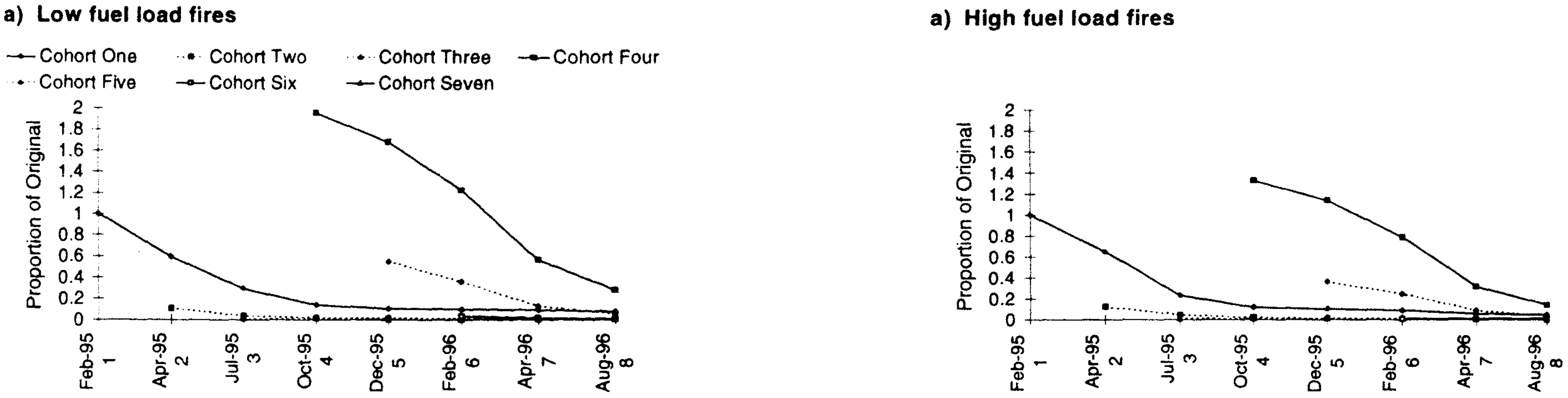


Figure 6.15. Proportional contribution of cohorts to the total population at the Arne degenerate stand.


a) Low fuel load fires

b) High fuel load fires

Figure 6.16. Proportional contribution of cohorts to the total population at the Aylesbeare degenerate stand.


a) Low fuel load fires

a) High fuel load fires

third cohort, which emerged between December 1995 and February 1996, was steeper than the curves for the other cohorts, indicating higher mortality. The first cohort exhibited the highest survivorship of the three cohorts. The differences between the paraffin treatments are not obvious on the graphs, but 'LIFETEST' revealed a significant difference in the first cohort (Table 6.13). In cohort two the log-rank statistic is significant but the Wilcoxon statistic is not, suggesting that the survivorship curves of the two treatments are only different towards the end of the monitoring period (summer 1996). In both cohorts, the survivorship was higher after fires with no paraffin than after the fires to which paraffin had been added (Fig. 6.17).

Table 6.12. Total number of seedlings in each cohort and treatment after 1995 fires at the Aylesbeare mature stand(4 plots).

Cohort	No paraffin added	Paraffin added
Oct 95 (1)	445	494
Dec 95 (2)	888	778
Feb 95 (3)	209	167
Apr 95 (4)	23	22
Aug 95 (5)	1	3

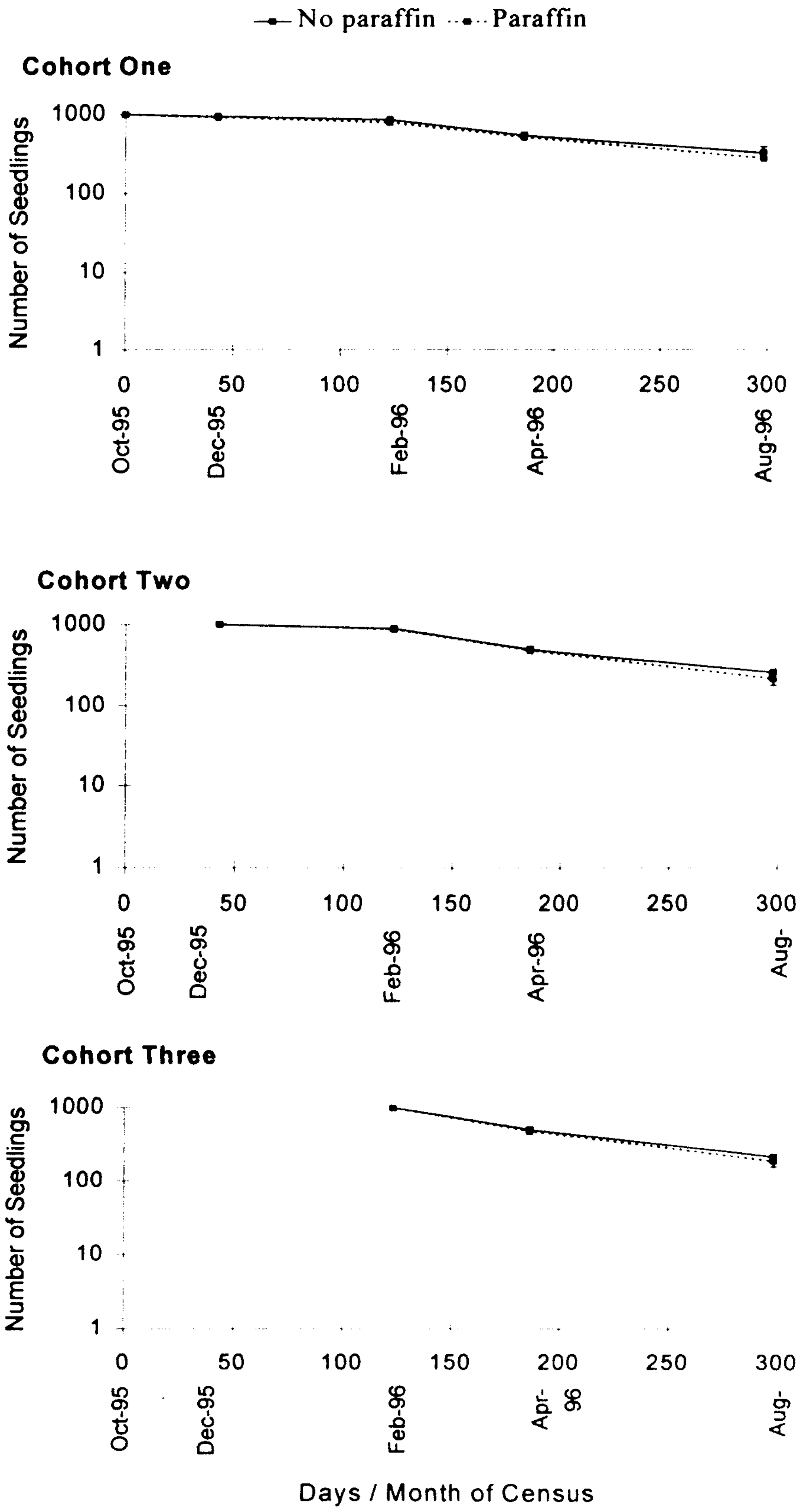
Table 6.13. 'LIFETEST' analysis of cohorts after 1995 fires at the Aylesbeare Mature stand. Wilcoxon and Log-rank $\chi2$ and significances are given. ** = $0.001 < P < 0.01$, * = $0.01 < p < 0.05$, NS = not significant.

Cohort	Log-Rank $\chi2$	Wilcoxon $\chi2$
Oct 95 (1)	6.38 *	5.86 *
Dec 95 (2)	7.65 **	3.62 NS
Feb 95 (3)	1.41 NS	0.86 NS

Population Flux

Changes in seedling density, emergence and death over time are shown in Figure 6.18. The results of a repeated measures ANOVA on these variables and on proportional mortality are in Table 6.14. There were no significant differences between treatments in any of the variables at any of the censuses. All variables

Fig. 6.17. Survivorship curves of ericaceous seedlings emerging after the 1995 fires at the Aylesbeare mature stand



varied significantly over time (Table 6.14). Seedling emergence peaked in November 1995 at about 2000 seedlings m^{-2} (Fig. 6.18a) and the number of seedling deaths was low until April 1996 (Fig. 6.18b). The number of seedlings that died in February 1996 was slightly less than the number of new seedlings that were observed at that census. Hence the population peaked in the winter at approximately 3000 seedlings m^{-2} (Fig, 6.18c). The decline in seedling density in the spring and summer was due to the death of existing seedlings and negligible emergence.

Figure 6.19 demonstrates that most of the population was made up of the first two cohorts.

Table 6.14. F-values generated by repeated measures ANOVA on the effects of burning different fuel loads on seedling emergence, death, density and proportional mortality after 1995 fires at the Aylesbeare mature stand. Huynh-Feldt adjustment was applied to probability values (p) of time, time x paraffin and time x block.

	Seedling Emergence		**Seedling Deaths**		**Seedling Density**		**Proportional Mortality**	
Source	**df**	**F**	**df**	**F**	**df**	**F**	**df**	**F**
Paraffin	1	0.13 NS	1	0.00 NS	1	0.09 NS	1	2.01 NS
Block	3	2.75 NS	3	3.77 NS	3	1.56 NS	3	1.79 NS
Time	4	27.71 ***	3	38.36 ***	4	66.80 ***	3	70.94 ***
Time x Paraffin	4	0.42 NS	3	0.40 NS	4	0.71 NS	3	0.11 NS
Time x Block	12	2.49 NS	9	2.17 NS	12	4.54 **	9	1.27 NS

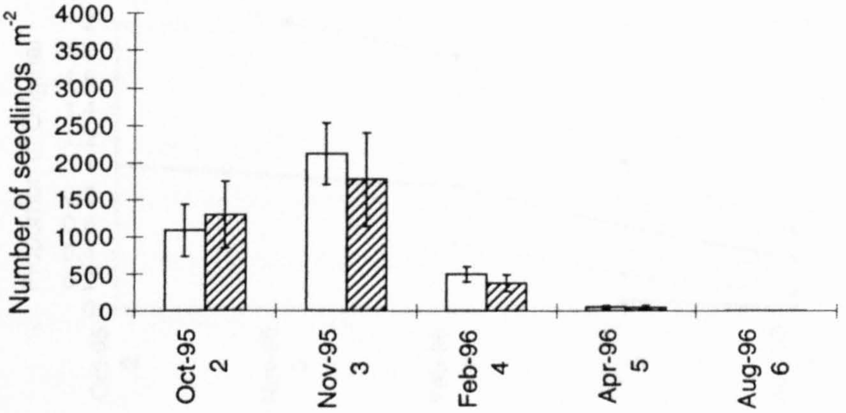
Proportional Mortality

Figure 6.20 and Table 6.14 show the absence of any effect of adding paraffin on the proportional mortality of seedlings that germinated after burning. Mortality was only about 10% in the winter of 1995 / 96 but increased to 0.4 - 0.55 in the summer 1996 censuses.

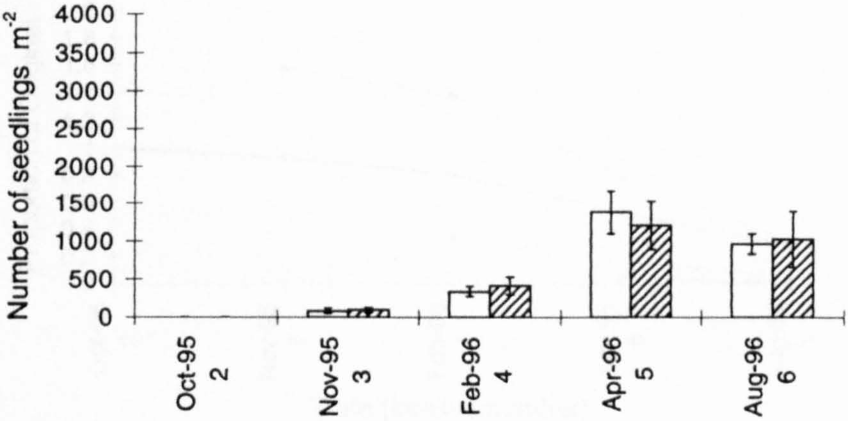
Fig. 6.18. Population Flux at the Aylesbeare mature stand (1995 Fires). Data are means ± 1 SE (n=4)

□ No paraffin ▨ Paraffin

a) Emergence



b) Deaths



c) Density

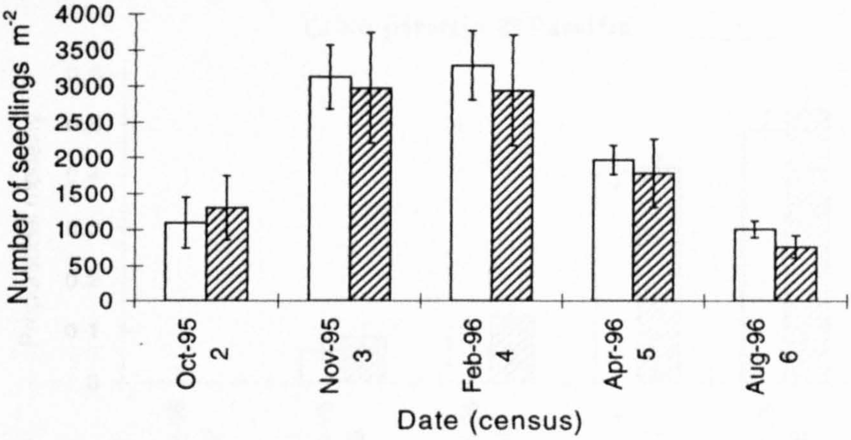
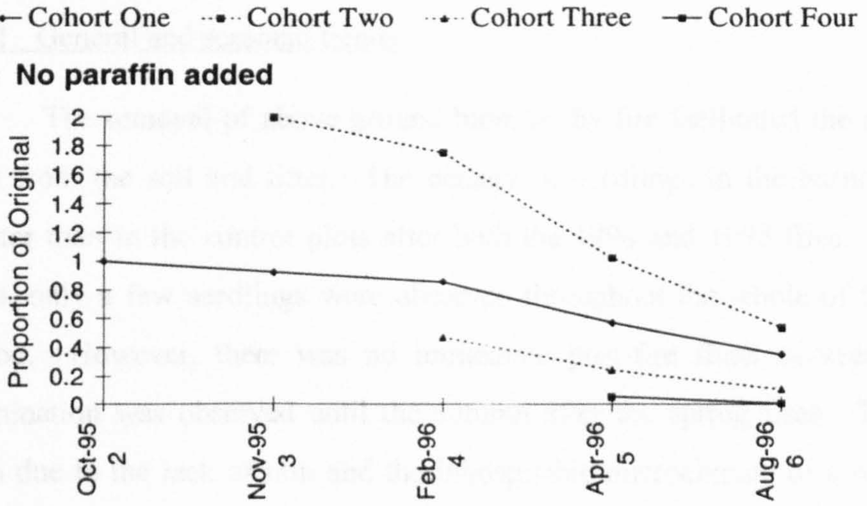


Fig. 6.19 Proportional contribution of cohorts to the total population at the Aylesbeare mature stand (1995 fires)

a) No paraffin added



b) Paraffin Added

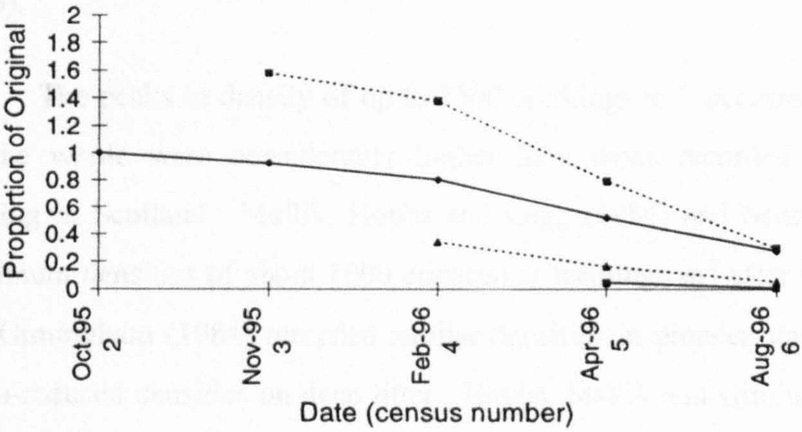
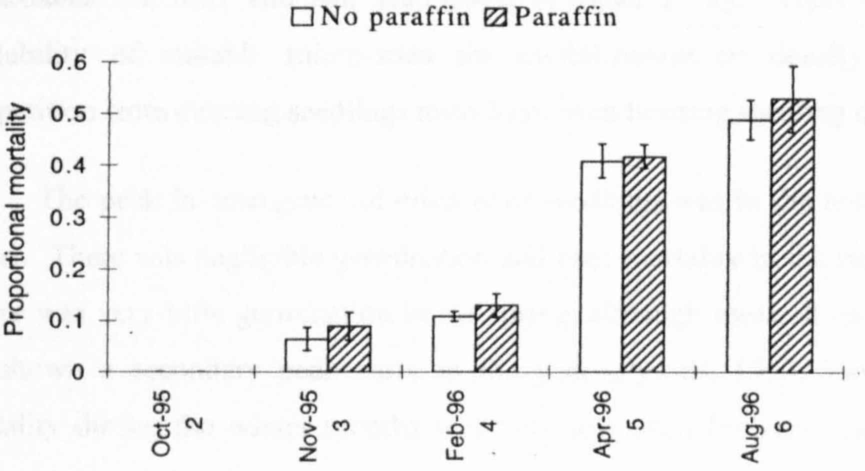


Figure 6.20 Proportional Mortality at the Aylesbeare mature stand (1995 fires). Mortality was calculated as the number of seedlings from all cohorts dying at census *t+1* as a proportion of the number alive at census *t*



6.4. Discussion

6.4.1. General and seasonal trends

The removal of above ground biomass by fire facilitated the germination of seed from the soil and litter. The density of seedlings in the burnt plots was far greater than in the control plots after both the 1994 and 1995 fires. In the control plots, only a few seedlings were observed throughout the whole of the monitoring period. However, there was no immediate post-fire flush of seedlings and no germination was observed until the autumn after the spring fires. This may have been due to the lack of rain and the inhospitable microclimate of a recently-burned surface. In addition, the deposited ash could have inhibited germination (Néeman, Meir and Néeman ,1993; Gonzàlez-Rabanal and Casal, 1995; Facelli and Kerrigan, 1996).

The peaks in density of up to 3500 seedlings m^{-2} occurred in the winter and on the whole were considerably higher than those recorded after management burning in Scotland. Mallik, Hobbs and Legg (1984) and Scandrett (1989) found maximum densities of about 1000 ericaceous seedlings m^{-2} after burning. De Hullu and Gimingham (1984) recorded similar densities in pioneer stands of heather, but much-reduced densities on deep litter. Hobbs, Mallik and Gimingham (1984) noted densities of only 20 *Calluna* seedlings m^{-2} one growing season after fire. Seedling densities after burning both in 1994 and 1995 may have been very high, but they did not exhaust the litter and soil seed pools (Chapter Four). Therefore, either the availability of suitable micro-sites for establishment or density - dependent competition from existing seedlings must have been limiting seedling density.

The peak in emergence of ericaceous seedlings was in the autumn and early winter. There was negligible germination and high mortality in the summer months. There was very little germination in the spring, although research on Dorset heaths has shown a secondary peak early in the year (Pywell, 1993; Traynor, 1995). Mortality during the winter months was very low even for very young seedlings, which persisted at the two cotyledon stage. However, on northern heathlands, where winters are more severe, frost and winter desiccation are major causes of seedling mortality (Mallik, Hobbs and Legg, 1984; Legg *et al.*, 1992; Aerts and Heil, 1993).

The graphs of proportional mortality in the 1994 experiment (Fig. 6.12) suggest that summer 1995 mortality was more severe at Arne than it was at Aylesbeare, with the Aylesbeare mature stand exhibiting the least mortality of all the stands throughout the monitoring period. There was rapid growth of *Agrostis curtisii* at this stand (Chapter Six) which may have ameliorated the microclimate. Summer temperatures of more than 40°C and low relative humidities of about 40% were recorded on the bare litter surface at Arne in 1996. The litter surface became very dry and cracks appeared in both summers of the monitoring period. Traynor (1995), investigating turf-cutting, also recorded lower seedling mortality at Aylesbeare than at Arne, and attributed this to the higher soil nutrient and water content and atmospheric humidity at this site. High summer mortality of ericaceous seedlings due to drought has also been observed by Miles (1972), Mallik (1984), Mallik *et al.* (1984), Legg *et al.* (1992), Pywell (1993), and Traynor (1995). Summer drought affects seedlings that germinate after fire in other habitats, including Californian Chaparral (Keeley and Zedler, 1978; Frazer and Davis, 1988), Australian shrublands (Abbott, 1985, Cowling and Lamont, 1987) and South African fynbos (Musil and de Witt, 1990).

It is likely that physical factors had more influence on mortality than density-dependent or age -specific factors. High mortality soon after germination is common in many plants, especially shrubs (Harper, 1977; Silvertown and Lovett-Doust, 1993). The mortality of all cohorts was highest in the summer months, although seedlings that survived one summer were less likely to die the following summer, perhaps because they had more developed root systems which enabled them to withstand drought (Legg *et al.* 1992). The weather data indicate that the summer of 1996 was wetter and began later than the summer of 1995 (Figs 6.19 and 6.20), so this may have also contributed to lower mortality in the second summer.

The extremely high mortality in the first summer after seedling emergence (1995) meant that some populations underwent a complete turnover in autumn 1995. Very few seedlings from the early cohorts survived and there was a peak in emergence in autumn 1995 (cohort four). The survivorship of cohorts four, five and six tended to be higher in their first summer (1996) than that of the earlier cohorts in 1995. The exception was the degenerate stand at Aylesbeare, where summer mortality was high for all cohorts. Both fuel load treatments at this stand burned at low intensity and a deep litter layer and unburned material remained after burning (Chapter Three). Loose litter acts as a physical barrier to emergence (Mallik, *et al.* 1988) and has poor water holding capabilities (Chapman and Rose 1979; de Hullu and Gimingham, 1984; Mallik *et al.*, 1988). Small-seeded species, such as *Calluna*, are especially susceptible to drought in deep litter because the seeds have very few reserves (Peterson and Facelli, 1992) and tend to die before the radicles can reach the soil (Purdie, 1977; Fowler, 1986). However, although there was a deep litter layer left after burning the degenerate stand at Arne, seedling survivorship here was no lower than in the low cover quadrats at the mature stand (Fig. 6.6).

Any differences in density and survivorship of the three ericaceous species cannot be elucidated, because most seedlings died before they became identifiable to species. Of the seedlings that were identified, there were very few *Erica tetralix* seedlings at the Aylesbeare mature stand, despite being frequent in the pre-fire vegetation and in the soil seed pool. Either there was negligible germination of this species, or most seedlings died before they could be identified. Bannister (1964) discovered low germination and establishment of E. tetralix on dry soils, so it seems likely that the post-fire environment was unfavourable for this species.

6.4.2. Effect of temperature on seedling density and survivorship

Fire temperature may affect the density of seedling germination directly by destroying some of the seed bank or by stimulating germination (Whittaker and Gimingham, 1962); or indirectly, by affecting soil nutrients and the post-fire microclimate. Microclimate may be influenced by the amount of unburnt stems and litter remaining after burning. For example, unburnt stems may provide some shelter for seedlings but the presence of too much unburnt material and a deep litter layer may hinder seedling germination and establishment (see section 6.4.1). The lack of effect of fuel load and hence fire temperature on seedling densities after the 1994 fires may be due to the variation in fire temperature and intensity within each plot as well as small-scale heterogeneity in seed banks, nutrient input and topography. It is likely that some seeds in the litter layer were killed by temperatures greater than 200°C (Whittaker and Gimingham, 1962) but the substantial soil and litter seed pools were not affected by burning (Chapter Four).

Fire temperature affected seedling survivorship at Arne but only in the high resprout cover quadrats at Aylesbeare. The similarity in seedling survivorship between treatments at the Aylesbeare degenerate stand is explained by the absence of any difference in temperature between the fuel load treatments. The seedling survivorship at both stands at Arne was higher after low fuel load fires than after high fuel load fires. The reasons for this are obscure, but may be due to differences in soil nutrients (Chapter Four), or indirect effects such as changes in soil water relations or deposition of unburnt material, which may have ameliorated microclimate. There may have been subtle effects of temperature on the substrate microtopography, influencing seedling survival (Harper, William and Sagar, 1965; Gimingham, 1972).

The addition of paraffin to mature heath at Aylesbeare in 1995 did not produce higher fire temperatures but seedling survivorship was higher after fires with no added paraffin. The addition of paraffin had a slightly adverse effect on seedling survival. No paraffin would remain on the soil after burning because it would have evaporated rapidly if any had remained uncombusted, so there is no obvious explanation for the effect on seedling survival.

6.4.3. Effect of resprout cover on seedling density and survivorship

At the mature stands, vegetative regeneration from rootstocks was observed soon after burning (Chapter Five). Seedling emergence began in the autumn following the spring fires. Therefore ericaceous seedlings had to compete with established resprouts (as well as *Agrostis curtisii* at Aylesbeare) for space, light and nutrients. Resprouting heather remains attached to the rootstocks deep in the soil, so is less affected by drought (Mallik *et al.* 1988). Although it competes with emerging seedlings, resprouting vegetation may offer shelter from micro-climatic extremes. The litter surface microclimate data from two plots at the Arne mature stand indicate greater fluctuation of temperature and relative humidity on bare ground than under resprouts. Therefore seedlings on bare ground may be more prone to desiccation in the summer and frost damage in the winter. Temperatures above 40°C were recorded, which are somewhat higher than those of Delany (1953), who recorded a maximum of 32.5°C on open ground and 24.25 °C at the base of *Calluna* bushes on heathland in Devon. Vaartaja (1949), working on wooded heath in Finland, measured maximum temperatures of 37 - 44 °C on the soil surface under *Calluna* bushes in contrast to a peak of 63°C on a burnt area. Mallik (1986) found temperatures up to 6°C higher on the soil surface of burned areas than under the heather canopy.

Seedling densities were lower in the high resprout cover quadrats than in the low cover quadrats, suggesting competition for space and other resources. The analysis revealed a significant interaction between resprout cover and time. Population densities in low resprout cover quadrats oscillated more than under resprout cover. The density of seedlings emerging under resprouts in October 1995, two growing seasons after fire, was less than that observed at the start of the monitoring period. In contrast, the bare ground densities were the same as, or greater than the starting densities. This implies that, as they grow, ericaceous resprouts (along with *Agrostis curtisii* at Aylesbeare) were having an inhibitory effect on seedling emergence.

Although resprout cover limited seedling densities, it increased the survival of the earlier cohorts. Survivorship of the first four cohorts at the Arne mature stand was higher in the high cover quadrats than in the low cover quadrats but there was no difference in the fifth and sixth cohorts. At the Aylesbeare mature stand all cohorts except cohort six showed significant differences but the effect was not as conspicuous as at Arne. The increasing density and height of resprouts over the monitoring period may explain the lack of difference in the later cohorts. Survivorship in the low cover quadrats may have increased as resprouting vegetation began to offer a more equable microclimate. However, the density and height of resprouts in and around the high cover quadrats may have increased to such levels as to adversely affect seedlings through competition and shading. It seems that conditions ideal for seedling establishment in the first growing season after fire were different to those favouring subsequent seedling survival (Miles, 1974b).

The effect of resprout cover was not as pronounced at Aylesbeare as it was at Arne probably because of the different species composition and resprouting success (Chapter Five). The rapid growth of *Agrostis curtisii* probably had a substantial influence on emerging seedlings, even at the beginning of the monitoring period. There was less bare ground at the mature stand at Aylesbeare than there was at the corresponding stand at Arne (Chapter Five) and the mean resprout cover in low cover quadrats was somewhat higher than it was at Arne (Table 6.4). This implies that the gaps between resprouting vegetation in the low cover quadrats were smaller than they were at Arne and the emerging seedlings were more sheltered from extremes of temperature and moisture (Miles, 1974a; de Hullu and Gimingham, 1984). It is possible that even at the beginning of the monitoring period the low cover quadrats were significantly affected by the surrounding vegetation. The seedling survival in both resprout cover categories at the Aylesbeare mature stand was the highest in the whole experiment, suggesting that the extensive regeneration of ericaceous shrubs and grasses that occurred at this stand helped to increase survivorship.

6.4.4. Conclusions

Fire temperature and intensity had no effect on the density of ericaceous seedlings that germinated after fire but the survival of these seedlings was enhanced by burning at lower temperatures. It is unlikely that temperature itself could influence seedlings that germinated more than six months after fire, so indetectable differences in the post-fire micro-environment may have been responsible.

The shelter offered by resprouting vegetation helped to increase seedling survival at the mature stands, although seedling densities were lower than on bare ground. However, there was evidence that, as resprouts grew, they began to out-compete seedlings. Therefore the density of seedlings emerging under the influence of resprouts is likely to decline with time and some of the seedlings already present may not survive.

The lack of vegetative regeneration at the degenerate stands meant that all seedlings were exposed to extremes of microclimate. Populations at the degenerate stands and in bare areas in the mature stands oscillated between wide limits. The instability of these populations implies a high risk of extinction. However, gradual re-establishment of cover only requires a few seedlings to survive to maturity and then spread by vegetative means.

The season when management burning is carried out may influence the relative contributions of seedlings and vegetative resprouts to overall regeneration. This work has shown that vegetative regeneration was vigorous in the first summer after spring fires but ericaceous seedlings did not germinate until the autumn. It may therefore be preferable to burn in the autumn to allow seedling establishment under less intense competition from resprouts. The growth of resprouts the following summer would provide shelter for the establishing seedlings. The time of burning may be even more important at the degenerate stands, where autumn burning may encourage immediate germination and allow seedlings to establish root systems before the summer drought.

CHAPTER SEVEN

General discussion

7.1. The effect of fuel load on fire temperature and intensity

The aim of this research programme was to investigate the impacts of management fires on the subsequent regeneration of heathland in relation to fire temperature. Fire temperatures were manipulated by either by altering fuel loads or by adding paraffin, and the effects of these on soil nutrients, seed banks, vegetative regeneration and seedling demography of ericaceous species were measured. Previous work on heathland fires has been carried out in Scotland (e.g. Kenworthy, 1963; Kayll and Gimingham, 1965; Hobbs and Gimingham, 1984 a and b; Hobbs *et al.*, 1984), where the objectives of management burning are somewhat different from those of the southern lowland heaths. The aim of burning in Scotland is to promote rapid regrowth of *Calluna* from stem bases to provide high quality grazing for sheep and grouse (Muirburn Working Party, 1977). Management of the southern lowland heaths is usually for conservation purposes, and burning is used to break up even-aged stands, arrest succession to scrub and maintain the impoverished nutrient status of the system (Gimingham, 1992).

The two study sites, Arne in Dorset and Aylesbeare in Devon (100km apart), differed in vegetation composition (Chapter Two), and therefore enabled a general perspective of responses to fires. The effect of the age of vegetation prior to burning on the resulting fire temperatures and regeneration was investigated by imposing fuel load treatments at stands of mature and degenerate growth phases of heath at both sites. Both the mature and degenerate stands at Arne were dominated by *Calluna* before burning. However, comparisons between the two stands at Aylesbeare had to take account of differences in vegetation composition.

The amount of fuel that was added or removed to create the high and low fuel load treatments in the 1994 fires was based on the difference between the mean biomass of the two stands at each site. This method was successful in creating significantly different fuel loads for the two treatments (Chapter Three) and the aim of manipulating fuel load was achieved: high fuel load fires burnt at significantly higher temperatures than low fuel load fires at all stands except at the Aylesbeare degenerate stand (Chapter Three). Fire intensity was highly correlated with fuel load consumed, therefore intensity was also significantly different between treatments and related to fire temperature.

The addition of paraffin in the 1995 fires was unsuccessful as a substitute for vegetation fuel load and there were no significant temperature differences between the two burning treatments. However, temperatures were higher than those in the low fuel load (umanipulated) 1994 fires at this stand (Chapter Three). This may have been due to differences in moisture contents of the fuel and weather just before and on the day of burning.

Fire temperatures were higher in the canopy than they were on the litter surface in both the 1994 and the 1995 experiments. Soil surface temperatures remained low at all stands, suggesting that the litter layer behaved as an efficient insulator and that there would have been no effect on stem bases or soil microbial processes (Raison *et al.*, 1986). Litter surface temperatures may affect the survival and germination of seeds (see section 8.4). Mean litter surface temperatures in the low fuel load fires in the first experiment were about 80°C at the Arne mature stand, but less than 50°C at the Arne degenerate and Aylesbeare mature stands (Chapter Three). Temperatures in the high fuel load fires were approximately double this, but mean temperatures were all below 200°C, the temperature at which *Calluna* seeds are killed (Whittaker and Gimingham, 1962). The hotter fires of the 1995 experiment recorded mean litter surface temperatures of about 200°C, and this may explain the depletion of the seed bank (see section 8.3).

Fire temperatures in the vegetation canopy determine the quantities of nutrients released in smoke. Nitrogen, carbon and sulphur are readily volatilised above 300°C (Kenworthy, 1963; Evans and Allen, 1971). Both treatments at the Arne mature stand experienced temperatures higher than 300°C, but at the Arne degenerate and Aylesbeare mature stands only the high fuel load treatment produced such high temperatures. The above-ground temperatures in the 1995 fires at the

Aylesbeare mature stand were about 450°C according to pyrometers and more than 600°C according to thermocouples.

7.2. The nutrient status after burning

Chapter Four describes the concentrations of phosphorus, potassium and calcium in the humic layer of soil and in the ash deposited on the litter surface. Previous studies have shown substantial losses of volatile nutrients (carbon, nitrogen and sulphur) in smoke at temperatures above 300°C (Kenworthy, 1963; Allen, 1964; Evans and Allen, 1971). In this study, it was not possible to calculate the quantities of nutrients lost in smoke, because there was no measure of the pre-burn content in the vegetation. In the 1994 experiment, fuel load and hence fire temperature / intensity had significant effects on the nutrient concentrations in the ash at all stands except the Aylesbeare degenerate stand. However, these differences were not consistent across stands (Chapter Four). The nutrient concentrations in the ash after burning at the Aylesbeare mature stand in 1995 were higher than in the control plots, but there was no difference between the two burning treatments, reflecting the lack of difference in fire temperatures.

Soil samples were taken immediately after burning, when there was no effect on the humic layer. The nutrient concentration in the humic soil may be expected to rise and then fall as nutrients are leached downwards (Allen, 1964). A more detailed study is required, with samples taken over a time series to determine the fluxes of the major plant nutrients. Nutrient levels at times critical to the plants, such as at the autumn peak in germination (Chapter Six) and during the summer would be particularly informative.

7.3. Seed banks and seedling establishment

The effects of fire on seed banks are described in Chapter Four. The seed bank provides the main source of propagules for regeneration after a disturbance such as fire (Miller and Cummins, 1987). Severe fires may destroy most of the seed bank and establishment of heathland vegetation then depends on aerial input of seed (Maltby *et al.*, 1990). There were no non-heathland species in the seed bank at any of the stands, implying that the appearance of such species in the regenerating vegetation would depend on aerial inputs or on seed migration through animals.

There was no effect of burning in 1994 on the density of seed in the litter or soil. There was no flush of germination and no increase in the density of the germinable seed bank after burning. Soil temperatures were so low that seeds in the soil would not have been affected by fire. Litter surface temperatures were variable, but some stimulation of germination may have been expected, according to the data of Whittaker and Gimingham (1962), who found that the percentage of seeds that germinated depended on the period of exposure. For example, temperatures of 40°C encouraged germination if exposure times were longer than 20 seconds. However, Mallik and Gimingham (1985) and Gonzãlez-Rabanal and Casal (1995) did not find a similar stimulatory effect on *Calluna*. There was no stimulation of germination after the 1995 fires at the Aylesbeare mature stand. The seed bank of *Erica tetralix* was depleted by a similar amount in both burning treatments but no other species were affected. This might suggest that *Erica tetralix* seeds are more sensitive to high temperatures than other species, but there has been no work to support this. Differential species responses may have implications for the succession after fire, but unless the seed bank is severely depleted, seedling density is more likely to be limited by physical conditions (Mallik *et al.*, 1988; Legg *et al.*, 1992).

In this study, the immediate post-burn soil / litter surface was probably unsuitable for establishment. Ericaceous species require moisture for germination (Pons, 1989) but the combination of a dry spring and the high evaporation rate of bare soil (Mallik *et al.*, 1988) would have led to moisture deficits. Summer temperatures on the bare litter surface at the Arne mature stand reached over 40°C (Chapter Six) and cracks in the surface were observed. In addition, the deposited ash could have inhibited germination (Néeman, Meir and Néeman ,1993; Gonzàlez-Rabanal and Casal, 1995; Facelli and Kerrigan, 1996).

The lack of an effect of fire temperature in the 1994 experiment on the seed bank was reflected in the absence of significant differences in seedling density between the two burning treatments. The density of seedlings observed at the first census in both experiments was smaller than the density of seeds available in the litter. The highest seedling densities were on bare ground at the Arne mature stand, where winter densities of about 3500 seedlings m^{-2} represented only 25% of the seed bank present in the litter layer. A similar percentage of the seed bank at the Aylesbeare mature stand germinated in the autumn following burning in 1995. At the Aylesbeare mature stand (1994 fires) 10 - 15 % of the available seed in the litter had established as seeds by the first census in February 1995 and less than 10% established at either of degenerate stands. This supports the estimation of Welch *et al.* (1990), that only 10 - 20% of seedlings in the top 5 cm of heathland soil would be exposed to light after disturbance. The density of seedlings after burning may have been limited by the inhospitable micro-environment or density-dependent competition.

7.4. Vegetative regeneration and succession

Regeneration at all stands in both experiments agreed with the 'initial floristic composition' model of succession (Egler, 1954, cited in Connell and Slatyer, 1977), with the same species present in the pre- and post-burn vegetation. There was no replacement of species by other species i.e. the 'relay floristics' model of Clements (1916; cited in Connell and Slatyer, 1977). At Aylesbeare, there was evidence to suggest changes in relative abundances of species over time, probably due to the individualistic responses of species to environmental factors such as drought and grazing (Pickett and McDonnell, 1989). The competitive abilities of the different species may change as the environment is modified (sensu the 'resource ratio' hypothesis of Tilman, 1988). However, it was not feasible to fully test these hypotheses because this study encompassed an early phase of succession and the trajectories may change over time.

Pre-burn stand age and possibly grazing affect post-burn vegetative regeneration, whereas fire temperature had no effect. The poor regeneration at the degenerate stands agrees with the work in Scotland by Kayll and Gimingham (1965), Grant (1968), Miller and Miles (1970) and Hobbs and Gimingham (1984b). However, *Erica cinerea* did resprout where present in the degenerate stands, and was co-dominant with *Agrostis curtisii* and *Ulex gallii* three growing seasons after burning at the Aylesbeare degenerate stand. Regeneration at the Arne degenerate stand was sparse and patchy, but the plants that were resprouting were growing vigorously and flowering prolifically.

Succession at the mature stands also depended on the species composition before burning. Calluna resprouted rapidly at Arne and flowered prolifically in the second and third growing seasons following burning (Chapter Five). Productivity was four times greater in the third growing season following burning than it was in either of the first two growing seasons. This difference may be due to the higher rainfall of 1996 compared with 1994 and 1995.

Succession at the Aylesbeare mature stand may have been influenced by selective grazing by rabbits and by the weather. The relative abundances of the species were different after burning than they were in the pre-burn vegetation. Total production by all species was similar in each year, but the ericaceous species may have been affected by the drought of 1995, because they showed very little increase in biomass between 1994 and 1995. *Erica tetralix* resprouted and flowered more vigorously than *Calluna* or *Erica cinerea* and appeared to have been avoided by rabbits. *Erica cinerea* comprised less than 10% of the total biomass and flowering was sparse in the three growing seasons of monitoring. *Calluna* was relatively less frequent after burning than before. *Erica tetralix*, *Ulex gallii* and *Agrostis curtisii* were co-dominant in the regenerating vegetation. There was evidence of a change in the relative proportions of species in the third growing season after burning (Chapter Five), with ericaceous species becoming relatively more abundant. The delayed increase in the abundance of ericaceous species has also been observed after heathland management fires in Scotland (e.g. Legg, 1978; Gimingham *et al.*, 1982; Mallik and Gimingham, 1983; Hobbs and Gimingham, 1984b) and after severe fire in Dorset (Gray, 1988).

The neighbouring plots burnt in the second experiment at this stand were only monitored for two years, but by the second growing season ericaceous species were already beginning to increase in relative abundance, although *Agrostis curtisii* was still common. The resprouting ericaceous plants showed fewer signs of grazing than they did at the plots burnt in 1994 and the 1995 drought appeared to have had little impact on production.

There was no effect of fuel load and hence fire temperature and intensity on vegetative regeneration after the 1994 fires. The range of temperatures generated by the fuel loads used were probably not sufficient to elicit a significant difference in vegetation response. This was probably due to the efficient insulation offered by the litter layer, which protected the stem bases from high temperatures.

The seedling demography study provided little information on species succession after burning, because only 25% of the ericaceous seedlings that germinated after the 1994 fires survived to a stage where they could be identified. Of the ericaceous seedlings that were identified, *Erica tetralix* represented only 2.6% at the Aylesbeare mature stand. This is of interest, because this species was co-dominant in the vegetation before burning, and resprouted more vigorously than the other two ericaceous species. Either *Erica tetralix* did not germinate in proportion to its available seed bank, or the seedlings that did germinate died before they could be identified. *Erica tetralix* is thought to be less tolerant of low moisture conditions than the other ericaceous species (Bannister, 1964; Pons, 1989).

7.5. Relative contribution of resprouting and seedling establishment to regeneration after fire (1994 fires only)

The relative contributions of seedlings and resprouts to regeneration after fire determine the speed of canopy development. There were significant differences in seedling survivorship between burning treatments in both experiments. The reasons for this are obscure (Chapter Six), because there was no effect of fire temperature on factors such as microclimate and litter depth which may affect seedling survival. The significant treatment difference in the nutrient concentration of the ash would be unlikely to still be significant a year after fire due to leaching (Allen, 1964; Smith, 1970). There were no fire treatment effects on seedling densities, but the resprouting vegetation at the mature stands burnt in 1994 had effects on both seedling densities and survivorship.

The percentage cover of bare ground at the mature stands declined steadily over the three seasons of monitoring (Chapter Five). Seedling densities were lower in the high resprout cover quadrats than they were in the low resprout cover quadrats. Summer mortality was high for both categories, but seedlings that survived one summer were more likely to survive the next summer (Chapter Six). Mortality of the first two cohorts was lower in the high resprout cover quadrats than in the low resprout cover quadrats. This suggests that the regrowth of the first growing season after fire increased the survivorship of seedlings that germinated in the following autumn and winter (cohorts one and two in Chapter Six) by protecting them from microclimatic extremes. There was less difference between low and high resprout cover quadrats in the survivorship of seedlings that germinated in the second autumn and winter after burning (cohorts four and five), and the density of seedlings that emerged seemed to be limited by the resprouting vegetation. This implies that the vigorous growth of resprouting vegetation prevented germination and establishment. Therefore resprouting vegetation appears to have favoured seedling survival for the first year after fire, but tall dense growth had an adverse effect and may eventually out-compete all the ericaceous seedlings. Therefore conditions ideal for seedling establishment in the first growing season after fire are different from those favouring subsequent establishment (Miles, 1974b). Seedlings may survive in gaps between resprouting bushes, benefit from the ameliorated microclimate offered by the surrounding vegetation and eventually develop into bushes. However, new genets will only make a small contribution to the total biomass when vegetative regeneration is successful. Long-term studies on gap dynamics are required to determine the factors influencing survival of establishing plants.

At the degenerate stands, where vegetative regeneration was sparse, seedlings may be expected to contribute more than resprouts to succession, but seedling survival was low (Chapter Six). The high summer mortality of seedlings at the degenerate stands was probably due to the deep (4 cm) litter layer preventing roots reaching the soil and causing seedlings to die of desiccation (Mallik *et al.*, 1988; Peterson and Facelli, 1992). The time taken for development of vegetation cover at the degenerate stands will depend on the rate of vegetative spread of the resprouting bushes and the accumulation of seedling populations. The presence of a seed bank and surrounding vegetation providing aerial inputs of seed should ensure flushes of germination every autumn. The eventual development of vegetation cover requires the establishment of only a few seedlings per m^2.

7.6. Conclusions and implications for management

The range of fuel loads tested in the first experiment produced fire temperatures and intensities sufficient to ignite most of the above-ground vegetation, except at the Aylesbeare degenerate stand. The 1995 fires at the Aylesbeare mature stand also removed most of the vegetation, whether or not paraffin was added. With the exception of the cool fires at the Aylesbeare degenerate stand, all fires were 'clean burns' and therefore achieved the desired outcome of management burning.

The drastic alterations made to fuel load produced significantly different fire temperatures, but this difference had little effect on regeneration (Table 7.1).

Table 7.1. The effects of fuel load on the main variables studied. + = high fuel > low fuel; - = high fuel < low fuel, x = no effect of fuel load.

Variable	**Arne**		**Aylesbeare**		
	Mature	**Degenerate**	**Mature**	**Degenerate**	**Mature 1995 Fires**
Fire temperature	+	+	+	x	x
Fire intensity	+	+	+	x	x
Seed bank	x	x	x	x	x *E. tetralix* depleted in both treats
P, K, Ca in humic soil	x	x	x	x	x
P, K, Ca in ash / litter	+	-	+	x	x both treats > controls
Regrowth biomass (all species)	x	x	x	x	x
Seedling Density	x	x	x	x	x
Seedling survivorship	-	-	differences not consistent	x	- 1st cohort only

The fire temperatures generated remained within the range of normal management fires (e.g. Whittaker, 1960; Hobbs and Gimingham 1984a; Hobbs and Gimingham, 1987). The unburnt stems and litter that remained at the degenerate stands may have hindered seedling establishment. Therefore more intense fires may be desirable at these stands. Adding vegetation fuel load to fill in gaps or burning at a different time of year may achieve this aim. Moisture contents in the vegetation and litter may be lower in autumn than in spring, producing fires of higher temperature and intensity. Seedling establishment may be favoured by burning in autumn, by altering the competitive balance between seedlings and resprouts. Seedlings would be expected to emerge soon after burning in the absence of resprouting vegetation and may benefit from elevated nutrient levels in the litter. The season of management burning on the southern lowland heaths requires further research.

There was a plentiful supply of propagules in the soil and litter seed bank, which was not affected by burning or fire temperature Seed bank studies should be carried out before management burning to determine whether there are propagules of invasive non-heathland species in the soil or litter. There were no non-heathland species in the seed bank at either Arne or Aylesbeare, but burning may not a suitable management technique at sites with a high proportion of such species in the seed bank, for example, heathland restored on ex-arable land (Pywell, 1993).

There was vigorous vegetative regeneration at both the mature stands at Arne and Aylesbeare. *Calluna* remained dominant at the Arne mature stand, but was relatively less abundant after burning at the Aylesbeare mature stand than it was before. There is evidence to suggest that the effect of burning on the relative abundances of species may interact with grazing and weather. Long-term studies on species succession after burning are required, especially with respect to grazing pressure.

The persistence of bare ground after burning degenerate stands of heath and the possibility of invasion by non-heathland species such as pine, birch and bracken (Gimingham, *et al.*, 1981; Hobbs, Mallik and Gimingham, 1985; Gong and Gimingham, 1984; Marrs, 1986) is one of the reasons for the decline in burning on the southern lowland heaths. However, there was no evidence of successional trajectories towards trees or bracken at either Arne or Aylesbeare. This may be a factor of the low nutrient status at these sites (Chapter Four), as well as the lack of a nearby source of propagules. Regeneration at the degenerate stands was patchy, but it is suggested that cover will eventually develop due to vegetative spread and seedling establishment. Furthermore, the presence of bare ground achieves one of the aims of management burning by creating structural diversity. Therefore burning is a valid management technique for degenerate as well as younger stands of heathland vegetation.

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APPENDICES

Appendix One: Means and ranges of temperatures recorded by pyrometers in each plot in the 1994 fires (Chapter Three)

Appendix Two: Nutrient and pH analytical procedures (Chapter Four)

Appendix Three: Results of ANOVAs on seedling population variables at individual censuses (Chapter Six)

APPENDIX ONE

Means ± 1 SE and ranges of temperatures recorded by pyrometers in each plot in the 1994 fires

Site	Soil Surface				Litter Surface				Maximum Above-Ground			
/Stand	Low Fuel Fires		High Fuel Fires		Low Fuel Fires		High Fuel Fires		Low Fuel Fires		High Fuel Fires	
Replicate	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Arne Mature												
1	24.0 ± 19.0	5-62	35.0 ± 16.5	5-62	59.0 ± 14.6	38-87	67.0 ± 18.4	38-101	371.0 ± 167	204-704	417.0 ± 149	204-704
2	35.0 ± 16.5	5-62	31.7 ± 13.9	5-52	59.0 ± 14.6	38-87	70.3 ± 8.30	62-87	232.0 ± 14.0	204-246	528.3 ± 92.7	343-621
3	54.0 ± 8.0	38-62	58.7 ± 3.3	52-62	114.3 ± 46.0	52-204	147.7 ± 53.5	62-246	621.0 ± 241	204-1038	676.3 ± 27.7	621-704
4	46.0 ± 14.6	38-87	133.0 ± 71.0	62-204	91.7 ± 4.7	87-101	366.0 ± 171	149-704	348.0 ± 179	135-704	704.0	704
Arne Degenerate												
1	24.0 ± 19.0	5-62	59.0 ± 21.0	38-101	64.3 ± 29.9	5-101	147.7 ± 53.5	62-246	152.3 ± 53.1	62-246	431.0 ± 139.0	246-704
2	5.0 ± 0.0	5	16.0 ± 11.0	5-38	71.7 ± 14.9	52-101	83.3 ± 11.4	62-101	264.3 ± 41.2	204-343	431.0 ± 139.0	246-704
3	5.0 ± 0.0	5	5.0 ± 0.0	5	36.3 ± 15.7	5-52	62.0 ± 0.00	62	156.7 ± 47.3	62-204	454.0 ± 250.0	204-704
4	5.0 ± 0.0	5	67.0 ± 18.4	38-101	20.7 ± 15.7	5-52	156.0 ± 47.1	87-246	322.0 ± 172	101-662	463.0 ± 120.0	343-704
Aylesbeare Mature												
1	5.0 ± 0.0	5	94.7 ± 21.4	62-135	5.0	5	146.7 ± 33.8	87-204	197.7 ± 74.0	101-343	463.0 ± 120.0	343-704
2	16.0 ± 11.0	5-38	43.0 ± 19.0	5-62	39.7 ± 17.6	5-62	70.7 ± 16.3	38-87	162.7 ± 21.1	135-204	185.7 ± 18.30	149-204
3	35.0 ± 16.5	5-62	36.3 ± 15.7	5-52	51.3 ± 24.3	5-87	58.7 ± 3.30	52-62	184.7 ± 61.3	62-246	551.0 ± 153.0	246-704
4	5.0 ± 0.0	5	43.0 ± 19.0	5-62	35.0 ± 16.5	5-62	78.7 ± 8.30	62-87	167.3 ± 18.3	149-204	385.0 ± 160.0	204-704
Aylesbeare Degenerate												
1	5.0	5	5.0	5	16.0 ± 11.0	5-38	16.0 ± 11.0	5-38	503.0 ± 201.0	101-704	158.0 ± 23.0	135-204
2	5.0	5	5.0	5	5.0	5	16.0 ± 11.0	5-38	313.0 ± 196.0	101-704	169.7 ± 34.3	101-204
3	5.0	5	5.0	5	35.0 ± 16.5	5-62	39.7 ± 17.6	5-62	300.0 ± 203.0	62-704	135.3 ± 34.3	101-204
4	5.0	5	5.0	5	20.7 ± 15.7	5-52	16.0 ± 11.0	5-38	88.0 ± 13.0	62-101	158.0 ± 23.0	135-204

APPENDIX TWO

Nutrient and pH analytical procedures

Soil pH

Approximately 25 ml of fresh soil and 25 ml of de-ionised water were added to a beaker, stirred and allowed to satnd for about 10 minutes. The pH was determined using a pH electrode buffered at pH 4.

Extraction of phosphorus, calcium and potassium from soil samples

Soil samples were digested by shaking 5 g of air -dried soil in 125 ml of 2.5% aqueous acetic acid for one hour on a rotary table shaker. Samples were left to stand for one hour before filtering through Whatman No. 42 filter paper.

Extraction of phosphorus, calcium and potassium from ash / litter samples

Ash and litter samples were digested by adding 10 ml of 4:1 perchloric acid to 1.5 g of sample in an acid-washed digestion tube. Tubes were left overnight to pre-digest and then placed on a digestor at 50°C for one hour. The temperature was then increased to 120°C for a further three hours. The tubes were removed from the digestor and left to cool before making up to 50 ml with double distilled water. The solutions were mixed thoroughly and then filtered through Whatman no. 42 paper.

Determination of phosphorus, calcium and potassium concentrations

The concentration of P in filtrates was estimated as a phosphomolybdate complex reduced by ascorbic acid using a Gilford Colorimeter. Calcium was determined using a Varian - Techtron 1275 atomic absorption spectrophotometer. Lanathium chloride was added to the extracts to reduce interferences due to aluminium, iron and phosphorus. Potassium was determined by flame emission. Caesium chloride was added to the extracts to suppress ionization of potassium in the flame.

APPENDIX THREE

Appendix 3.1. ANOVAs on individual censuses showing the effects of burning different fuel loads on seedling emergence, death and density at Arne Mature. F values and significances are shown. F = fuel load, B = block, R = resprout cover. MS fuel load x block used as denominator to calculate F-value of fuel load and block.

		Census							
Source	**df**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Emergence									
Fuel Load	1	0.23 NS	0.08 NS	26.33 **	0.59 NS	0.22 NS	109.24 **	0.63 NS	0.00 NS
Block	2	1.28 NS	0.11 NS	99.50 **	0.71 NS	33.30 *	58.59 *	1.75 NS	0.25 NS
Fuel x Block	2	2.76 NS	6.66 NS	0.07 NS	1.54 NS	0.26 NS	0.00 NS	0.12 NS	1.67 NS
Resprout cover	1	27.49 **	7.63 NS	0.20 NS	25.65 **	57.31 **	4.94 NS	0.28 NS	1.06 NS
Fuel x Resprout	1	0.40 NS	1.48 NS	0.37 NS	0.13 NS	1.27 NS	1.46 NS	0.07 NS	0.55 NS
Deaths									
Fuel Load	1		2.15 NS	0.00 NS	1.25 NS	0.59 NS	0.13 NS	1.40 NS	0.75 NS
Block	2		1.97 NS	0.14 NS	2.61 NS	0.18 NS	1.54 NS	8.41 NS	1.55 NS
Fuel x Block	2		5.12 NS	38.88 **	2.55 NS	1.69 NS	1.35 NS	0.08 NS	0.58 NS
Resprout cover	1		20.80 *	29.08 **	0.22 NS	22.60 **	24.18 **	6.46 NS	9.62 *
Fuel x Resprout	1		0.87 NS	1.24 NS	0.06 NS	0.21 NS	0.09 NS	0.42 NS	0.15 NS
Density									
Fuel Load	1	0.23 NS	0.16 NS	1.29 NS	0.10 NS	0.02 NS	0.01 NS	0.03 NS	0.00 NS
Block	2	1.28 NS	0.13 NS	2.10 NS	0.67 NS	1.38 NS	1.50 NS	1.14 NS	1.13 NS
Fuel x Block	2	2.76 NS	22.79 **	2.36 NS	2.20 NS	1.76 NS	1.70 NS	2.21 NS	2.63 NS
Resprout cover	1	27.49 **	14.59 *	0.01 NS	18.67 *	23.16 **	25.18 **	18.57 *	12.48 *
Fuel x Resprout	1	0.40 NS	0.20 NS	0.03 NS	0.00 NS	0.03 NS	0.09 NS	0.32 NS	0.20 NS
Proportional Mortality									
Fuel Load	1		62.04 *	9.33 NS	0.21 NS	1.07 NS	0.17 NS	0.57 NS	0.67 NS
Block	2		10.08 NS	13.80 NS	12.51 NS	1.00 NS	1.73 NS	1.51 NS	1.45 NS
Fuel x Block	2		0.61 NS	0.54 NS	0.14 NS	2.28 NS	0.98 NS	0.59 NS	0.52 NS
Resprout cover	1		4.12 NS	2.26 NS	0.29 NS	1.77 NS	0.01 NS	0.11 NS	0.09 NS
Fuel x Resprout	1		2.75 NS	0.26 NS	0.07 NS	1.18 NS	0.44 NS	0.36 NS	0.00 NS

Appendix 3.2. ANOVAs on individual censuses showing the effects of burning different fuel loads on seedling emergence, death and density at Aylesbeare Mature. MS fuel load x block used as denominator to calculate F-value of fuel load and block

		Census							
Source	**df**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Emergence									
Fuel Load	1	0.05 NS	5.14 NS	0.82 NS	5.23 NS	10.79 NS	0.71 NS	30.34 *	1.00 NS
Block	2	3.21 NS	13.73 NS	4.52 NS	33.94 *	142.18 **	10.18 NS	27.33 *	82.95 *
Fuel x Block	2	1.44 NS	0.73 NS	0.10 NS	0.26 NS	0.04 NS	0.61 NS	0.18 NS	0.02 NS
Resprout cover	1	21.94 **	17.08 *	0.45 NS	83.39 **	21.24 *	7.92 *	0.01 NS	7.83 *
Fuel x Resprout	1	0.20 NS	0.27 NS	0.37 NS	0.26 NS	0.01 NS	1.00 NS	8.35 *	0.02 NS
Deaths									
Fuel Load	1		0.04 NS	0.08 NS	5.00 NS	0.83 NS	13.83 NS	8.93 NS	0.08 NS
Block	2		7.54 NS	4.99 NS	11.05 NS	2.17 NS	14.63 NS	34.99 *	43.48 *
Fuel x Block	2		1.90 NS	5.21 NS	0.28 NS	9.15 *	1.41 NS	0.87 NS	0.09 NS
Resprout cover	1		21.51 **	33.30 **	17.56 *	217.20 ***	76.86 **	93.17 **	22.27 **
Fuel x Resprout	1		3.73 NS	1.31 NS	0.22 NS	3.29 NS	0.13 NS	0.09 NS	0.02 NS
Density									
Fuel Load	1	0.05 NS	0.48 NS	1.55 NS	4.60 NS	14.99 NS	8.84 NS	4.07 NS	2.49 NS
Block	2	3.21 NS	4.87 NS	2.34 NS	6.29 NS	30.92 *	24.65 *	13.13 NS	3.10 NS
Fuel x Block	2	1.44 NS	0.66 NS	0.17 NS	0.44 NS	0.15 NS	0.17 NS	0.12 NS	0.19 NS
Resprout cover	1	21.94 **	11.47 *	4.71 NS	51.96 **	59.19 **	54.26 **	16.93 *	6.21 NS
Fuel x Resprout	1	0.20 NS	0.03 NS	0.00 NS	0.11 NS	0.08 NS	0.10 NS	0.10 NS	0.19 NS
Proportional Mortality									
Fuel Load	1		0.21 NS	0.11 NS	8.13 NS	0.00 NS	8.83 NS	1.30 NS	0.81 NS
Block	2		22.39 *	4.45 NS	3.34 NS	3.15 NS	11.17 NS	20.68 *	3.48 NS
Fuel x Block	2		0.20 NS	0.52 NS	8.44 *	1.06 NS	5.13 NS	0.48 NS	0.30 NS
Resprout cover	1		0.05 NS	0.10 NS	80.05 ***	3.76 NS	0.01 NS	2.53 NS	2.27 NS
Fuel x Resprout	1		0.71 NS	0.17 NS	11.23 *	0.20 NS	0.00 NS	0.06 NS	0.15 NS

Appendix 3.3. Nested ANOVAs on individual censuses showing the effects of burning different fuel loads on seedling emergence, death and density at Arne, comparing the two stands. The high cover quadrats at the mature stands were not used in the analysis. MS Block (Stand) used as denominator to calculate F value of Stand.

		Census							
Source	**df**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Emergence									
Stand	1	7.07 NS	8.08 *	0.10 NS	23.88 **	0.53 NS	4.48 NS	11.56 *	0.23 NS
Fuel load	1	2.12 NS	0.55 NS	2.04 NS	1.87 NS	0.13 NS	0.29 NS	0.50 NS	0.75 NS
Block (stand)	4	0.54 NS	0.25 NS	2.31 NS	1.75 NS	8.04 *	2.15 NS	0.96 NS	0.91 NS
Stand x Fuel load	1	1.97 NS	0.95 NS	0.52 NS	3.73 NS	2.60 NS	1.72 NS	0.51 NS	0.03 NS
Deaths									
Stand	1		6.04 NS	7.41 NS	0.42 NS	4.59 NS	0.00 NS	2.29 NS	8.70 *
Fuel load	1		0.00 NS	0.62 NS	3.22 NS	0.79 NS	0.16 NS	0.23 NS	0.34 NS
Block (stand)	4		1.35 NS	0.51 NS	0.94 NS	2.55 NS	10.49 *	10.07 *	2.80 NS
Stand x Fuel load	1		4.46 NS	1.07 NS	0.84 NS	6.49 NS	0.51 NS	0.35 NS	0.05 NS
Density									
Stand	1	13.15 *	9.21 *	0.61 NS	17.72 *	5.82 NS	8.63 *	9.11 *	7.77 *
Fuel load	1	2.12 NS	1.80 NS	3.20 NS	1.88 NS	1.01 NS	1.16 NS	1.42 NS	3.02 NS
Block (stand)	4	0.54 NS	0.27 NS	0.83 NS	1.38 NS	2.07 NS	1.80 NS	1.34 NS	1.54 NS
Stand x Fuel load	1	1.97 NS	0.99 NS	0.77 NS	2.96 NS	1.77 NS	2.03 NS	1.85 NS	3.89 NS
Proportional Mortality									
Stand	1		7.23 NS	1.07 NS	5.89 NS	637.38 ***	74.20 **	13.39 *	12.55 *
Fuel load	1		4.36 NS	0.07 NS	1.30 NS	0.15 NS	1.62 NS	1.38 NS	5.53 NS
Block (stand)	4		3.35 NS	5.51 NS	5.69 NS	0.19 NS	1.19 NS	1.60 NS	1.54 NS
Stand x Fuel load	1		28.13 **	6.76 NS	4.01 NS	1.58 NS	1.41 NS	1.33 NS	3.41 NS

Appendix 3.4. Nested ANOVAs on individual censuses showing the effects of burning different fuel loads on seedling emergence, death and density at Aylesbeare, comparing the two stands. The high cover quadrats at the mature stands were not used in the analysis. MS Block (Stand) used as denominator to calculate F value of Stand.

		Census							
Source	**df**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Emergence									
Stand	1	7.64 NS	3.58 NS	4.09 NS	0.51 NS	0.11 NS	7.87 *	0.01 NS	1.00 NS
Fuel load	1	0.68 NS	2.50 NS	0.69 NS	0.36 NS	1.20 NS	5.15 NS	2.06 NS	0.08 NS
Block (stand)	4	0.52 NS	0.83 NS	2.37 NS	1.87 NS	2.73 NS	3.58 NS	0.12 NS	1.00 NS
Stand x Fuel load	1	0.11 NS	0.04 NS	0.21 NS	2.26 NS	2.34 NS	13.43 *	0.87 NS	1.00 NS
Deaths									
Stand	1		0.41 NS	0.00 NS	1.42 NS	0.00 NS	2.00 NS	0.10 NS	1.32 NS
Fuel load	1		1.61 NS	2.10 NS	0.30 NS	1.20 NS	5.15 NS	2.06 NS	0.08 NS
Block (stand)	4		3.74 NS	1.65 NS	2.98 NS	1.71 NS	4.05 NS	5.46 NS	1.05 NS
Stand x Fuel load	1		0.30 NS	0.41 NS	1.01 NS	3.56 NS	5.52 NS	3.19 NS	0.30 NS
Density									
Stand	1	7.64 NS	4.44 NS	19.63 *	4.14 NS	2.76 NS	6.92 NS	7.86 *	9.22 *
Fuel load	1	0.68 NS	1.01 NS	0.22 NS	0.32 NS	0.24 NS	0.06 NS	0.01 NS	0.00 NS
Block (stand)	4	0.52 NS	0.80 NS	0.44 NS	0.83 NS	1.14 NS	1.03 NS	1.27 NS	1.24 NS
Stand x Fuel load	1	0.11 NS	0.22 NS	0.00 NS	1.55 NS	1.58 NS	1.41 NS	1.22 NS	1.49 NS
Proportional Mortality									
Stand	1		0.48 NS	14.23 *	1.81 NS	1.11 NS	9.50 *	3.33 NS	12.34 *
Fuel load	1		0.10 NS	1.11 NS	3.42 NS	0.07 NS	4.91 NS	0.73 NS	0.07 NS
Block (stand)	4		4.35 NS	1.16 NS	5.44 NS	2.01 NS	5.95 NS	4.71 NS	0.40 NS
Stand x Fuel load	1		1.03 NS	0.70 NS	3.62 NS	0.03 NS	0.67 NS	0.08 NS	0.53 NS

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