CHAPTER 1

Introduction to the research

1.1 Research aims

Although the native Caledonian pinewoods of Scotland are currently dominated by Scots pine (*Pinus sylvestris*[1]), evidence suggests that native broadleaved tree species were formerly a more important constituent of this vegetation type (Malcolm, 1957; Steven & Carlisle, 1959; McVean & Ratcliffe, 1962; Rodwell, 1991; Rodwell & Patterson, 1994; Peterken, 1996; Anon, 2003a). Little is known concerning the ecological behaviour of broadleaved trees in the pinewoods, yet such information is critical to the success of current ecological restoration[2] initiatives in these woodlands in Scotland.

The main aims of the thesis were:

i) to quantify shade tolerance in Scottish native woody species in relation to physiological responses

ii) to understand how broadleaved seedlings / saplings (planted stock & natural regeneration) establish and grow within different developmental stages of *P. sylvestris* woodland.

An achievement of these aims will help develop understanding of the role of the broadleaf component and shade tolerance in Caledonian forest dynamics. The research will predominately focus on the concept of shade tolerance because it acts as a very useful performance parameter. Its quantification involves the analysis of a spectrum of species responses to the interaction of light, nutrients and water thus taking into account, multiple resource limitation theory (Chapin *et al*., 1987) and the way that growth and survival is modified from site to site.

1.2 The Caledonian Forest

1.2.1 Definition, history & conservation value

The term, *Caledonian Forest* traditionally describes the ancient forest of Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) that was believed once to have covered a large proportion of the Scottish Highlands (McVean & Ratcliffe, 1962). Pinewood

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[1] Nomenclature follows Stace (1999) for all species henceforth.

[2] Restoration is defined here to mean rehabilitation where the objective is a renewal of ecosystem health and recovery and management of ecological integrity and functioning.

coverage has fluctuated a lot since its establishment approximately 8500 years ago. This fluctuation has been attributed to both environmental factors and anthropogenic activity (Steven & Carlisle, 1959; Bennett, 1995; Worrell, 1996, Smout, 2003). During the Holocene, 8000 years ago, a decline in pine in SW Scotland occurred as a result of competition with broadleaved trees especially oak and alder (Bennett, 1995). Four thousand years ago, a massive contraction of Scots pine began in NW Scotland where pine forest was replaced with bog and heathland. This *era of pine decline* has been linked primarily to regional climate change due to broad-scale features of global atmospheric circulation increasing precipitation levels and thus promotion of the expansion of blanket bog. As recently as the 14th to 17th Century, the reduction or disappearance of pinewoods has been attributed partly to climatic conditions (increased rainfall, strong storms and colder winters) experienced in the Little Ice Age (Wolff & Tipping, 1999; Smout, 2003).

Natural causes of pine decline throughout history are acknowledged but it is also clear that anthropogenic activity, such as deforestation, burning and over-grazing by cattle, sheep and deer has played a serious part in Caledonian forest decline (McKenzie & Callander, 1995). At the time of the Roman invasion of Britain, it is estimated that the Caledonian Forest covered some 1.6 M ha of the Scottish Highlands. By the beginning of the 1990's, this area had been reduced to around 16,000 ha of genuinely native pinewood. It is often stated that this represents one percent of the former extent (Aldhous, 1995; Featherstone, 1997; Anon, 2003a). However, Smout (2003) believes such figures are meaningless as they relate to woodland cover 5000 years ago in totally different climatic conditions.

Today, only remnants of the Caledonian Forest are found in the Scottish Highlands in just 84 separate areas (Anon., 1998). They are now protected, due to recognition of their high conservation value. They are valued due to their awesome beauty, unique genetic structure and their habitat value (Aldhous, 1995; Newton & Humphrey, 1997). Caledonian forest remnants are representatives of the oceanic boreal forest type (Worrell, 1996) with notable sub-alpine flora and fauna (Steven & Carlisle, 1959). Examples of pinewood fauna include the pine marten, wildcat and rare and endangered bird species such as the Golden Eagle, Scottish Crossbill and Capercaillie. The orchid, *Goodyera repens*, and the moss *Ptilium crista-castrensis* are believed to be true representatives of Caledonian pinewood flora (Pitkin *et al.*, 1995).

1.2.2 Composition and structure

Scots pine (*P. sylvestris* var. *scotica* (Willd.) Schott) dominates the canopy, with birch (mainly *B. pubescens* in the west and *B. pendula* in the east) and rowan (*Sorbus aucuparia*) as the most common associated tree species (Rodwell, 1991). These associated trees are typically infrequent and can be found as scattered individuals under moderately closed pine canopies or in thicker patches where the cover is more open. Birch and, in some places, oak are most common where pinewoods integrate with other woodland communities. In these transitional communities, holly (*Ilex aquifolium*) is also found in close association with the pine (especially in the milder west), whilst in other cases, juniper (*Juniperus communis*) may be present as scattered bushes. Where the pinewoods also include valley and basin mires, other broadleaves such as alder (*Alnus glutinosa*), willow (*Salix*) and aspen (*Populus tremula*) are found, although not over extensive areas.

Today, most broadleaves tend to be less integrated within the native pinewoods (Rodwell, 1991; Worrell, 1996). Instead they are found in separate bioclimatic or edaphic zones. Rodwell (1991) frequently mentions how birch has invaded ground that was previously occupied by mixed pine forest. Segregation is believed to be a result of indirect and direct human influences such as selective removal of broadleaved trees (Malcolm, 1957; Peterken & Stace, 1987; Summers *et al*., 1997; Smout, 2003) and overgrazing by deer restricting natural regeneration (Edwards & Nixon, 1999). Many researchers believe that broadleaves were formerly a more important constituent of the native pinewoods (Malcolm, 1957; Steven & Carlisle, 1959; McVean & Ratcliffe, 1962; Rodwell, 1991; Rodwell & Patterson, 1994; Peterken, 1996; Smout, 2003):

> *The terrain that now carries pure pine probably grew mixed pine, birch forest with abundant alder, rowan, willow, aspen, bird cherry and juniper, with scattered oaks and with a good mixed age composition in the various constituents.*
>
> McVean, 1964

Indeed, analysis of pollen from cores has shown that ancient native pinewoods, like Abernethy Forest (O'Sullivan, 1977) and East Glen Affric (Wolff & Tipping, 1999) had a higher percentage of broadleaved trees than they do today.

1.2.3 Dynamics

The dynamics of woodland communities are inextricably linked with the scale, pattern and frequency of natural disturbance (Pickett & White, 1985). A distinction is frequently made between fine-grained ‘gap phase’ dynamics and coarser scale ‘stand replacement’ dynamics although in practice these represent two points on a continuum of spatial and temporal scales (Quine *et al*., 1999). In gap dynamics, the structure of the forest is dominated by small gaps caused by the death of one or several trees and an all aged mixed forest structure can develop. Stand replacement dynamics refers to the formation of larger patches (ranging from 1-1000 ha) caused by extensive fires, storms and insect pests which can lead to the development of even-aged stands.

Originally, stand replacement dynamics and large disturbance regimes were considered to play a dominant role in structuring oceanic pine and birch forests (Worrell, 1996). There are a number of factors which support this viewpoint.

i) The Caledonian pinewoods are typically made up of a mosaic of quite well segregated age-classes, rather than being an intimate mixture of tree of all ages (Rodwell, 1991).

ii) The different age-class stands that exist within pinewoods have been described as more or less even-aged (McVean & Ratcliffe, 1962; Worrell, 1996). Pinewoods have been described as having an amoeboid habit:

> *Fir woods do not spring from the Root, but are propogated by the blowing of the seed in the Grounds, immediately adjacent to the old woods, or in Openings, where they have Freedom of Air, these highland Fir-woods are not fixed to a particular spot, but gradually shift their Stances.*
>
> Mitchie (1901)

Peterken (1985) also describes how pine and birch woodland boundaries expand, contract and even move in body over long periods.

iii) There is evidence to suggest that fires were once widespread in Scottish pinewoods and were important in creating suitable conditions for *P. sylvestris* establishment (O’Sullivan, 1977; Nixon & Clifford, 1995).

Now, it is acknowledged that the role of major windstorms and fires may have been exaggerated in the past and the role of small gap replacement underestimated (Worrell, 1996). In today's wetter climate, fire is believed to be more limited, contributing as a disturbance agent only on drier sites in the east (Worrell, 1996). Wind, instead is believed to be more important (Peterken, 1989; Worrell, 1996) which can have a low and high impact on the landscape (Quinn *et al*., 1999; Humphrey, 2003). In Glen Affric, it has been estimated that 18% of the most sheltered parts of the reserve would be classed as within the gap-phase, 25% in more exposed areas would lie in the stand replacement class and 42% in a transitional zone between the two (Mason & Humphrey, 1999). As well as wind, snow storms, fire from lightning strikes, insect attack, grazing and tree felling can generate a mixture of small and large disturbances influencing the structure of Scottish pinewoods (Cameron, 1995). A mosaic of well-segregated age classes is described. McVean & Ratcliffe (1962) and McVean (1964) noted three arrangements: even-aged 80-150 years old, two generation mixtures 150-200/80-100 years olds; and pine heaths with trees 150-200 years old. Ring core analysis of trees within pinewood remnants has revealed how trees are concentrated in the 150-300 year age-classes (Nixon & Clifford, 1995; Arkle & Edwards, 1996). Furthermore, trees in the 50-100 year classes are extremely limited, reflecting the widespread lack of regeneration during this period, which has largely been due to intense grazing pressure (Nixon & Clifford, 1995).

Man has altered the pinewoods so much that the nature of post-disturbance dynamics in Scottish pinewoods can only be surmised or inferred from studies of similar Eurasian boreal forest ecosystems (Steijan & Zackrisson, 1987; Kuusela, 1992; Engelmark *et al.*, 1994). Rodwell (1991) states that what does seem certain is that, in the past, progression to pine woodland involved a greater contribution from other native tree species.

The original patchwork of mixed dominance have been widely accepted as playing an important role in reversing podzolization (Malcolm, 1957; Miles, 1985; 1988; Wilson & Campbell, 1996; Emmer *et al.*, 1998) with species like birch and juniper being less active encouragers of mor than pine (Rodwell, 1991). Malcolm (1957) describes in detail how *Betula*, *Sorbus aucuparia*, *Alnus glutinosa* and *Ilex aquifolium* counter the inherent degrading tendency of *P. sylvestris* due to the acidity of its litter. *Betula*, for example, has a reputation as a "soil improver", known to reduce soil acidity and increase A horizon depth due to organic matter incorporation (Patterson, 1993; Wilson & Campbell, 1996). This in turn provides more favourable conditions for Scots pine seed germination which prefers well drained mineralised soils (McVean, 1963a).

Oliver's (1981) stand development model for post-disturbance forest dynamics has been used as a framework to help understand structural development in the absence of major disturbance in Caledonian pinewood (Oliver, 1981; Oliver & Larson, 1996; Mason & Humphrey, 1999). The four main stages have been outlined in Table 1.1 with suggestions of structural and compositional changes of tree species and understorey vegetation. Wind disturbance (low and high impact) has also been built into the Oliver model to help understand its effect on pinewood stand development (Humphrey, 2003).

Table 1.1 General stages of stand dynamics and their application to Scots pine forests (Oliver, 1981; Oliver & Larson, 1996). Details on stand age, habitat type (Mason & Humphrey; 1999), understorey vegetational changes (Rodwell, 1991; Humphrey, 2003) and tree species compositional changes (Peterken, 1996) are given.

Development stage	Age range	Description
1. Stand initiation	0-10/20	Establishment stage: After a disturbance or removal of deer grazing, young trees seed in and colonise open ground for a few years. Tree colonisers include birch, pine, and juniper. *Calluna* decreases and grasses increase.
2. Stem exclusion	10/20-60/80	Thicket-pole stage: Saplings grow so branches interlock or overtop weaker neighbours; closing the canopy which creates lower light conditions. Intolerant species, i.e: pine & birch, grow rapidly to form a canopy while more tolerant species such as rowan grow more slowly to from a diffuse underwood. Aspen forms dense clones, particularly on rock outcrops. Vegetation is shaded out except for bryophytes.
3. Understorey re-initiation	60/80-c.150	Scots pine canopy begins to open up because of increased height of trees and mortality of suppressed trees. Canopy vigour declines, allowing advance regeneration to grow up creating a more diverse canopy structure with sub-canopy thicket layers (eg: Birch, Oak, Alder). *Calluna* and *Vaccinium* increase.
4. Old growth	>150	Old growth canopy starts to break up and die in an irregular fashion, adding dead wood to the ecosystem. This generates new gaps and patches are generated, allowing sub-canopy regeneration to grow towards upper storey. On infertile patches, mixed Scots pine and birch predominate while on more fertile patches (in the past), mix of Scots pine and more tolerant broadleaves (e.g: Oak). *Vaccinium* declines but *Calluna* increases. Bryophytes increase together with fungi on dead and dying trees.

1.2.4 Regeneration

Disturbance events and subsequent colonisation by plant species are of prime importance in structuring tree populations but the regenerative phase has frequently been identified as playing a central role in plant demography (Grubb, 1977; Swaine & Lieberman, 1987; Grime & Hillier, 1992). Thus recent research on tree demography has focused on the regeneration phase of tree species in an attempt to identify one or more of the factors which influence their abundance and spatial distribution. The requirements for establishment of any species are the production of viable seed and its dispersal to a potentially suitable microsite, followed by suitable conditions for germination and seedling survival and growth.

In the Scottish Highlands, overgrazing by mainly sheep and deer is widely accepted as the major limitation to tree seedling establishment (Cummins, 1982;

Miller *et al*., 1982; 1998; Stains, 1995; Beaumont *et al*., 1995; Ramsay, 1996; Miller & Cummins 1998; Harmer & Gill, 2000). Other factors which also limit regeneration include the lack of a seed source (Miles, 1988) and mycorrhizal associations (Miles & Kinnaird, 1979; McVean, 1963a; Crowell, 1998); pests and pathogens (McVean, 1963b); nutrient deficiency; (Malcolm, 1957; McVean, 1963b; Miles, 1974a; 1985; Crowell, 1998); desiccation (McVean, 1963b; Miles & Kinnaird, 1979); water-logging with anoxia (Malcolm, 1957; McVean, 1963b; Crowell, 1998); ericaceous species including *Calluna vulgaris* (Handley, 1963; Jalal & Read, 1983a, 1983b; deHullu & Gimingham, 1984; Leake, 1992; Mallik, 1995) and competition for light (Kinnaird, 1974).

McVean (1963b) suggests that the combination of inadequate illumination, faulty mineral nutrition and competition from other plants for available nutrients are the commonest causes of sapling mortality. Once the threat of browsing by deer has been removed, these factors probably do play a substantial role. If so, it is feasible to suggest that the ability to tolerate shade under an array of fluctuating resources would be a valuable asset.

1.2.5 Shade tolerance

Shade tolerance has been defined as an ability to survive and maximise carbon gain in the understorey (Spurr & Barnes, 1998) or persist in deep shade for a period of time (Grime, 1966; Greene *et al*., 1999). The concept is highly influential among forest ecologists, because interspecific differences in tolerance are widely believed to drive secondary succession in forests (Horn, 1971; Bazzaz & Pickett, 1980; Whitmore, 1982; Shugart, 1984).

The mechanisms behind secondary succession in forests and species diversity are often centred around the concept of gap regeneration dynamics (Whitmore, 1990; Spurr & Barnes, 1998). It involves the universal forest cycle where trees fall down and seedlings regenerate in gaps. The traditional theory proposes that different species are specifically adapted to regenerate in gaps of a particular size. Swaine and Whitmore (1988) proposed a division of tropical tree species into two groups: shade tolerant climax and shade intolerant pioneer species based on their different light requirements for seed germination and seedling establishment. Shade tolerant climax species germinate and establish in the shade whilst shade intolerant pioneers require full sunlight for germination. Theory states that slow growing shade tolerant climax species will replace the shade intolerant pioneers in the absence of major disturbance (Shugart, 1984; Spurr & Barnes, 1998).

In real terms, the pioneer-climax dichotomy represents two extreme responses in an ecological continuum. Within the climax group, species will range from being extremely shade tolerant to more light demanding (Canham, 1989; Whitmore, 1989). At one extreme, there are species whose seedlings are very persistent in deep shade and are released, either with no or only small increases in light, such as occurs in a tiny canopy gap. At the other extreme, there are species whose seedlings persist only under light shade and are released by substantial increases in light. The identification of the above broad species guilds supports gap size / niche differentiation, one concept (out of many) which contributes to explanations on the maintenance of tropical forest diversity (Burslem *et al*., 2001).

Temperate tree species have been classified into understorey tolerant and understorey intolerant groups. The term "shade" from shade in/tolerance has been removed, to emphasise the influence of other environmental factors besides light on the ability to growth and survival in the shade (Spurr & Barnes, 1998). A continuum of tolerance amongst species from one extreme to the other is acknowledged as in the tropics. In America, there is a five point scale of tolerance including very tolerant, tolerant, intermediate, intolerant and very intolerant species (Baker, 1949). In Europe, there is a nine point scale based on Ellenberg's light indicator values (see Section 1.2.6).

Peterken (1996) recognises two types of shade tolerance strategy[3]: i) species which grow steadily in shade but do not respond to periods of increased light and ii) those that persist in shade without net growth but respond strongly to gap formation (facultative species). Delucia *et al*. (1998) has sub-divided these groups further into species that promote persistence, species that maximises growth in the understorey and species that promote maintenance of a high potential for exploiting canopy gaps. Intolerants have been divided into two sub-groups: i) short term opportunists which can not withstand shade and quickly occupy sites that become available after disturbance; ii) and species which persist on extreme and very infertile sites, where they withstand repeated disturbance by drought or the cold by means of rapid regeneration or very slow growth (Peterken, 1996).

Temperate tolerants and intolerants share climax and pioneer regeneration characteristics, similar to their tropical counterparts. Both groups have specific morphological and physiological traits which enable them to maximise survival and /

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[3] The use of the term "strategy" throughout the thesis follows Grime's definition as "a grouping of similar or analogous genetic characteristics which reoccur widely amongst species or populations and caused them to exhibit similarities in ecology" (Grime, 1979). It should not be interpreted as an ability to carefully plan towards an advantage or desired end.

or growth in their respective habitats (Table 1.2). Pioneers, for example, are able to colonise large gaps and open areas rapidly due to rapid wind or animal dispersal of abundant light seed, followed by rapid germination and growth (Swaine & Whitmore, 1988; Schupp *et al*., 1989; Whitmore, 1990; Popma *et al*., 1992; Kitajima, 1994; Peterken, 1996). Physiological adaptations reflect selection pressures for high photon flux densities with high saturation rates of photosynthesis and high rates of respiration, smaller leaf areas, higher chlorophyll a:b ratios and lower levels of photosynthetic pigments in leaf epidermal layers (Bazzaz, 1979; Mulkey *et al*., 1996). Generally, intolerants have a higher degree of phenotypic plasticity[4] than tolerants which enables them to maintain a positive carbon balance for rapid growth and survival in their more variable and unpredictable environment (Grime, 1979; Strauss Debenedetti & Bazzaz, 1991; Chazdon, 1992; Press *et al*., 1996; Veneklaas & Poorter, 1998).

Shade tolerant climax species produce large seed reserves which aid survival for long periods in the shade (Table 1.2). The morphological and physiological adaptations of shade tolerant climax species general reflect selection pressures to maximise quantum yields and light absorption while minimising carbon costs in the shade (Bazzaz, 1979; Givnish, 1988; Mulkey *et al*., 1996). Carbon costs are minimised by low saturation rates of photosynthesis, low light compensation points and low rates of respiration so little net photosynthesis is needed to bring rates of CO_2 evolution to zero. Thin leaves with smaller investments of dry weight and mineral nutrients per unit area reflect lower costs of construction and maintenance (Bongers & Popma, 1990; Popma *et al*., 1992). Low root mass ratios, low leaf turnover rates and longer leaf life spans also conserve carbon (Bongers & Popma, 1990). Quantum yields and thus growth rates can be optimised by the maintenance of a high specific leaf area (SLA) (leaf area per leaf mass), high leaf area ratio (LAR) (leaf area per plant mass) and low root: shoot ratios (Horn, 1971; Givnish, 1988).

Traits to maximise energy capture, however, are not always found in shade tolerants due to different strategies and a trade-off between energy capture and susceptibility to herbivores, pathogens and others sources of mortality such as water stress (Spurr & Barnes, 1998; Kitajima, 1994; Delucia *et al*., 1998; Veneklaas & Poorter, 1998). Some species maintain large roots in the shade to resist drought in water-stressed environments (e.g.: *Quercus rubra*) (Spurr & Barnes, 1998) or to store carbohydrates for rapid growth following a canopy disturbance (e.g.: *Prunus*

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[4] Phenotypic plasticity is the property of a given genotype to produce different physiological and morphological phenotypes in response to different environmental conditions (in Callaway *et al*., 2003).

serotina) (Delucia *et al*., 1998). Other species have strategies for persistence where low SLA and LAR contribute to low growth rates but also confer resistance to herbivory and pathogens (e.g: *Acer saccharum*) (Delucia *et al*., 1998).

Table 1.2 The main characteristics of pioneer (intolerant) and climax (tolerant) tree species. From Spurr & Barnes (1998); Bazzaz (1979); Swaine & Whitmore (1988); Whitmore, (1990); Kitajima (1994); Mulkey *et al*. (1996).

	PIONEER (INTOLERANT)	CLIMAX (TOLERANT)
GERMINATION	Only in canopy gaps open to the sky which receive some full sunlight	Usually below canopy
SEEDLINGS	Cannot survive below the canopy	Can survive below the canopy
SEEDS		
Seed size	Small and light	Often large
Production	Copious	Not copious
Soil seed bank	Many species	Few species
Dispersal	By wind or animals often over considerable distances	By diverse means, including gravity, sometimes only a short distance
Dormancy	Orthodox	Recalcitrant
PHYSIOLOGY		
Compensation point	High	Low
Light saturated rates of photosynthesis	High	Low
Sunfleck photosynthetic efficiency	Low	High
Respiration rates	High	Low
Stomatal conductance	Low	Higher
Photosynthetic Nitrogen Use Efficiency (PNUE)	High	Low
Photosynthetic Phosphorus Use Efficiency (PPUE)	High	Low
Phenotypic plasticity	Generally high	Generally low
GROWTH & MORPHOLOGY		
Height growth	Fast	Often slow
Relative growth rate	High	Lower rates
Leaf area ratio (LAR)	Variable but generally smaller	Variable, depending on strategy, herbivore susceptibility
Specific leaf area (SLA)	Variable but generally smaller	Variable, depending on strategy, herbivore susceptibility
Root : shoot ratio	Low, allows seedlings to grow up quickly in high light	Variable, depending on water & nutrient availability
Branching	Sparse, few orders	Often copious, often several orders
Leaf life span	Short, high turn-over rate	Long, slow turn over rate
Longevity	Often short	Sometimes very long
Ecological Range	Wide	Sometimes narrow
Herbivory	Leaves susceptible, soft, little chemical defence	Leaves sometimes less susceptible due to mechanical toughness or toxic chemicals

Classifications in British native tree species have mainly been based on subjective observation supported by very little quantitative research. Thus, shade tolerance and its role in Scottish native woodlands is poorly understood. One may argue that shade tolerance is not an important factor driving succession in the Caledonian pine forest because it is perceived to be a fairly open woodland ecosystem predominated by light-demanding pioneer species. Traditional classifications do suggest that the native broadleaves and evergreens lie towards the intermediate and intolerant end of the shade tolerance spectrum (Ellenberg, 1988; Savill, 1998; Hill *et al*., 1999). However, this in itself identifies a range of responses to light with potential differences in shade tolerance and plasticity influencing spatial distribution patterns.

Within the Caledonian pinewood ecosystem, light can be very heterogeneous with seedlings subjected to deep shade in closed swards of grass, *Calluna* and bracken communities closely associated with the woodlands. The light environment will also change across stands of varying structure in stand development (Table 1.1) and where pinewood merges with other woodland types. Questions about shade tolerance are becoming more relevant with the recent acknowledgement of gap phase dynamics in pinewoods (Nixon & Clifford, 1995). Furthermore current policy requires managers of conifer plantation forests to increase the diversity of their stands through, amongst other options , the use of native broadleaved species during the restocking process. It is acknowledged that these native species need to be self-sustaining to be of any benefit to the attainment of multiple purpose objectives such as the enhancement of biodiversity and maintenance of habitat "nodes" for expansion (Mason *et al.*, 1999). Successful underplanting of self-sustaining native tree species within conifer plantations (including plantations on ancient woodland sites (PAWS) (Thompson *et al.*, 2003) requires a knowledge of the shade tolerance ability or light demand of a particular species.

1.2.6 Ellenberg light indicator values

Ellenberg (1988) defined a set of indicator values for vascular plants based on observations on the field distributions of species in Central Europe. Environmental values include light indicator values where plants have been assigned a rank on a scale of 1-9: from very low light (1) to full daylight (9) (Table 1.3). The scale can be related to a tolerance range, ascending from most shade tolerant (1) to shade intolerant (9) with intermediates between. Recently the Ellenberg system has been extended to British plant species (Hill *et al*., 1999, 2000). New values were calculated by comparing original indicator values of species with the mean values of their associated species. The new light indicator values for canopy tree species refer to the sapling stage. However, these new values for saplings are not considered totally reliable due to a lack of species found in samples when surveying in British woodland understorey, which limited comparisons (M.O. Hill, personal communication). In this thesis, both the original Ellenberg light indicator values and Hill's adjusted values will be used as a baseline for comparison when quantifying shade tolerance in different Scottish native tree species. It is acknowledged that revised indicator values based on physiological responses may not necessary relate to Ellenberg indicator values based on natural spatial distribution patterns.

Table 1.3 Ellenberg's light indicator values (Ellenberg, 1988). Light value i.e: position in the gradient from very low illumination (1) to full light (9).

1	Plants in deep shade, may be less than 1%, seldom more than 30% relative illumination
2	Between 1 & 3
3	Shade plants, mostly less than 5% relative illumination., but also in lighter places
4	Between 3 & 5
5	Plants of half shade, rarely in full light but generally more than 10% relative illumination
6	Between 5 & 7
7	Plants generally in well lit places but also occur in partial shade.
8	Light-loving plants, rarely found where there is less than 40% relative illumination.
9	Plants of full light, found only in full sun; rarely in less than 50% relative illumination

1.3 Restoration policy and practices

The international agreements made at the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro in 1992 and the commitments signed at Helsinki in 1993 initiated international policy on the sustainable management of the world's forests. This led to the promotion of sustainable forestry (Anon., 1994) and biodiversity (Anon., 1995) in UK forest policy. As a consequence, the conservation and restoration of Caledonian forest has become a government priority. These native woodlands have been listed as priority habitats for conservation in the UK Biodiversity Action Plan (Anon., 1995) as well as in the European Union Habitats Directive (Council Directive 92/43/EEC of May, 1992). The latter has led to legal protection of designated sites as Special Areas of Conservation (SNH, 1995) and to EU funding for restoration projects (Council Regulation EEC No. 1973/92). Long term management plans are now required for increasing diversity in habitat and age, as well as the maintenance of biodiversity and ecological functions to comply with the UK forestry standard or to receive certification under the UK Woodland Assurance Scheme (UKWAS Steering Group, 2000).

Devolution of the Scottish parliament in 1999 has led to much change within the British Forestry Commission and its delivery of forest policy. On April 1st, 2003, Forestry Commission Scotland came into being. Its main aim is to deliver the Scottish Forestry Strategy "Forests for Scotland" (Anon. 2000) which will guide the development of Scotland's expanding forest and woodland area into the 21st Century and beyond.

> *"The vision is that Scotland will be renowned as a land of fine trees, woods and forests which strengthen the natural environment and which people enjoy and value"*

The Scottish Forestry Grant Scheme (SFGS) (Anon., 2003b) was launched in 2003 to aid delivery of the Scottish Forestry Strategy. Objectives within the various grants include support for the re-creation and restoration of the native pinewoods. Stewardship grants, for example, which encourage activities in existing woodlands, are available for native woodland (including the pinewoods), improving woodland biodiversity and reducing deer numbers.

Information which has been published to aid private owners with re-creation and restoration of pinewoods includes the Forestry Practice guide, *Native Pinewoods* (Anon, 2003a) and *Creating New Native Woodlands* (Rodwell & Patterson, 1994). Furthermore a PC based tool called the Ecological Site Classification Decision Support System has recently been released which classifies the quality of a site (based on climatic and edaphic factors) to aid the choice of appropriate tree species and woodland types (Ray, 2001; Pyatt *et al*., 2001).

In the operational guidelines for native pinewoods, general management principles include the need to increase diversity of structure and species where appropriate and maintain diversity of habitat (Anon, 2003a). Natural regeneration is strongly preferred to planting as it conserves local genotype and favours the natural distribution of tree species in relation to site conditions. The natural regeneration of species other than pine which are encouraged include birch, alder, willow, rowan, holly, juniper, oak, hazel and aspen. If planting is undertaken, it must be with stock that originates from the same locality and reflects local genetic diversity.

Since 1991, a bias has developed towards the re-creation of native woods with less attention being given to the restoration of existing native woodland remnants (Pryor, 2003). This is quite perplexing, as one would think it more logical to start with the restoration of existing stands as they provide a source for further expansion. Native pinewoods today are in a degenerative state, and an improvement in current conditions (i.e.: through broadleaf establishment) is paramount to kick start dynamics and conserve their biodiversity. The disparity between recreation and restoration has been highlighted, and thus the later may have some chance in becoming a strategic priority in the future (Humphrey *et al*., 2003).

1.4 Practical implications of the research

Management guidelines stress the importance of restoring pinewoods to their natural state, which involves the enhancement and maintenance of structural and compositional biodiversity. To implement such objectives, more information is needed on how well broadleaves establish on different sites within the Caledonian forest in present-day conditions. This information may question and/or improve forest practice guidelines and management tools. Furthermore information on the shade tolerance of native tree species and establishment probabilities can be used as important parameters in forest growth models which are being developed to understand the dynamics and successional development of forest communities in Scotland.

1.5 Presentation of the thesis and its objectives

The work is structured in seven chapters. There are four main research chapters that follow the main introduction and study site descriptions. They are specifically dedicated to achieving the following objectives:

i) to determine how one-year-old seedlings of 15 Scottish native woody species differ in their growth, allocation and morphology when established under different simulated forest shade regimes (Chapter 3);

ii) to explore and explain the relationship between relative growth rate in woody species and irradiance (Chapter 4);

iii) to determine how one-year-old seedlings of four Scottish native broadleaved species differ in their growth, allocation and morphology when established under different developmental stages of *P. sylvestris* woodland (Chapter 5);

iii) to determine how naturally regenerating *S. aucuparia* seedlings differ in spatial and temporal growth patterns between gap and shade habitats within an old-growth *P. sylvestris* woodland (Chapter 6).

The achievement of these objectives was aided by answering specific research questions:

i) Do species show classical responses to shade in accordance with the literature? (Chapters 3, 4 & 5)

ii) Which morphological, physiological or environmental variables play important roles in driving relative growth rates across different irradiances or pinewood stand types? (Chapters 3 & 5)
iii) How can differences in growth, allocation and morphology be used to distinguish different degrees of shade tolerance amongst species? (Chapters 3, 4 & 5)
iv) How well do physiological responses match traditional notions of shade tolerance and Ellenberg light indicator values? (Chapters 3 & 5)
v) How do spatial distribution patterns, abundance, age, size and growth of naturally regenerating *S. aucuparia* differ between gap and shade habitats? (Chapter 6)
vi) How does the growth of naturally regenerating *S. aucuparia* differ between gap and shade microhabitats over time? (Chapter 6)
vii) Does the abundance of *Calluna vulgaris* have a negative impact on the establishment of tree seedlings? (Chapters 5 & 6)
viii) How is shade tolerance modified in the field? (Chapter 7)

The final chapter (Chapter 7) summarises, compares and discusses results from the four main sections. It clarifies how this research has contributed to the quantification of shade tolerance in Scottish native tree species and to an understanding of broadleaf establishment under Caledonian pine. Furthermore the role that shade tolerance and the broadleaf component have to play in Caledonian pinewood dynamics are discussed. Proposals to improve native pinewood forest practice guidelines and / or aid pinewood restoration management (especially within the Glen Affric reserve) are clearly stated.