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Forest and woodland dynamics

5. WOODLAND REGENERATION WITH EXAMPLES DRAWN FROM INVESTIGATIONS OF OAK WOODLAND

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The meaning of the term "regeneration", as applied to woodlands, extends beyond mere reproduction to include germination of propagules and subsequent growth and survival of young trees until they are reasonably established (ie the immediate probability of mortality is low). This usage is in accord with the dictionary definition 'to bring into renewed existence'. Also, because the term is rarely applied to individuals but rather to populations of trees (ie woodlands), the study of regeneration may be regarded as an exercise in population dynamics. Old trees die, or are harvested, and are then replaced by young trees by:

true natural regeneration—regeneration that occurs without the intervention of man,

'foresters' natural regeneration—regeneration contrived by the use of different silvicultural practices, eg the uniform shelterwood system, the group selection system

artificial regeneration—regeneration by planting young trees grown in nurseries.

These different types of regeneration have many features in common, eg with all of them it is usually necessary to control grazing by domestic or wild animals for at least a short period. Even true natural regeneration may require control of herbivores as large predators have often been eliminated or their numbers greatly depleted.

To maintain the species, a tree, like other plants and animals, must ensure the survival of at least one offspring in its lifetime (on average). Thus the emphasis shifts from the high rate of success sought in agriculture, eg crops such as wheat and potatoes, to the ultimate survival of a very few individuals. In true, as opposed to 'foresters', natural regeneration, the time-scale and a surplus of replacements for silvicultural requirements, eg to encourage straight, clean (branch-free) stems and provide an intermediate harvest, are largely irrelevant. Nonetheless, reproduction is an extremely critical stage in the life process and the penalty of failure is to be replaced by another species of tree or vegetation with some other life-form. In rare cases, where reproduction fails to keep pace with mortality, extinction of species occurs. However, trees are an extreme example of reproductive longevity. Individual trees of a species such as oak may live for up to 400 years and are capable of reproducing for all but the first 25-30 years. This reproductive strategy has obvious advantages; the repeated production of seed maximising the chance of coincidence with favourable conditions for establishment (cf some bamboo species which exhibit synchronous flowering over a large area followed by death).

The difficulties of investigating the population dynamics of woodlands are considerable, the main problem being that of time-scale. Ecological changes in woodland take place very slowly and without careful, systematic recording it is difficult to determine what is happening—if anything. Sometimes it is easier to observe change in retrospect. For example, an area of woodland in north Wales gave the appearance of being even-aged. However, a study of ring growth showed that there was an age range from 100-150 years and that natural regeneration, at quite a modest density, had produced this area of woodland but had taken at least 50 years to do so. Even though this was a fairly dramatic example of non-woodland being replaced by woodland (historical evidence and early growth rates indicate this transformation), it is doubtful whether what was happening would have been obvious to the casual observer at the time.

Clearly straightforward observational or experimental investigation of woodland dynamics is out of the question because of the time-scale involved. To obtain an understanding in a reasonable period of time it is necessary to piece together evidence from the different processes involved and it is therefore essential to identify the more critical processes. For sessile oak *(Quercus petraea)* in north Wales, the most critical part of the cycle is seedling growth and survival and, in this instance, grazing by sheep is the single most important factor influencing these processes. Most woodlands in north Wales are unfenced (or ineffectively fenced) and are subject to severe grazing and browsing pressures for at least 6 months (December-June) of the year. Unless they are protected by other species less favoured for food e.g. hawthorn *(Crataegus monogyna)* or perhaps birch (*Betula* spp), or are inaccessible to sheep, eg on cliffs,

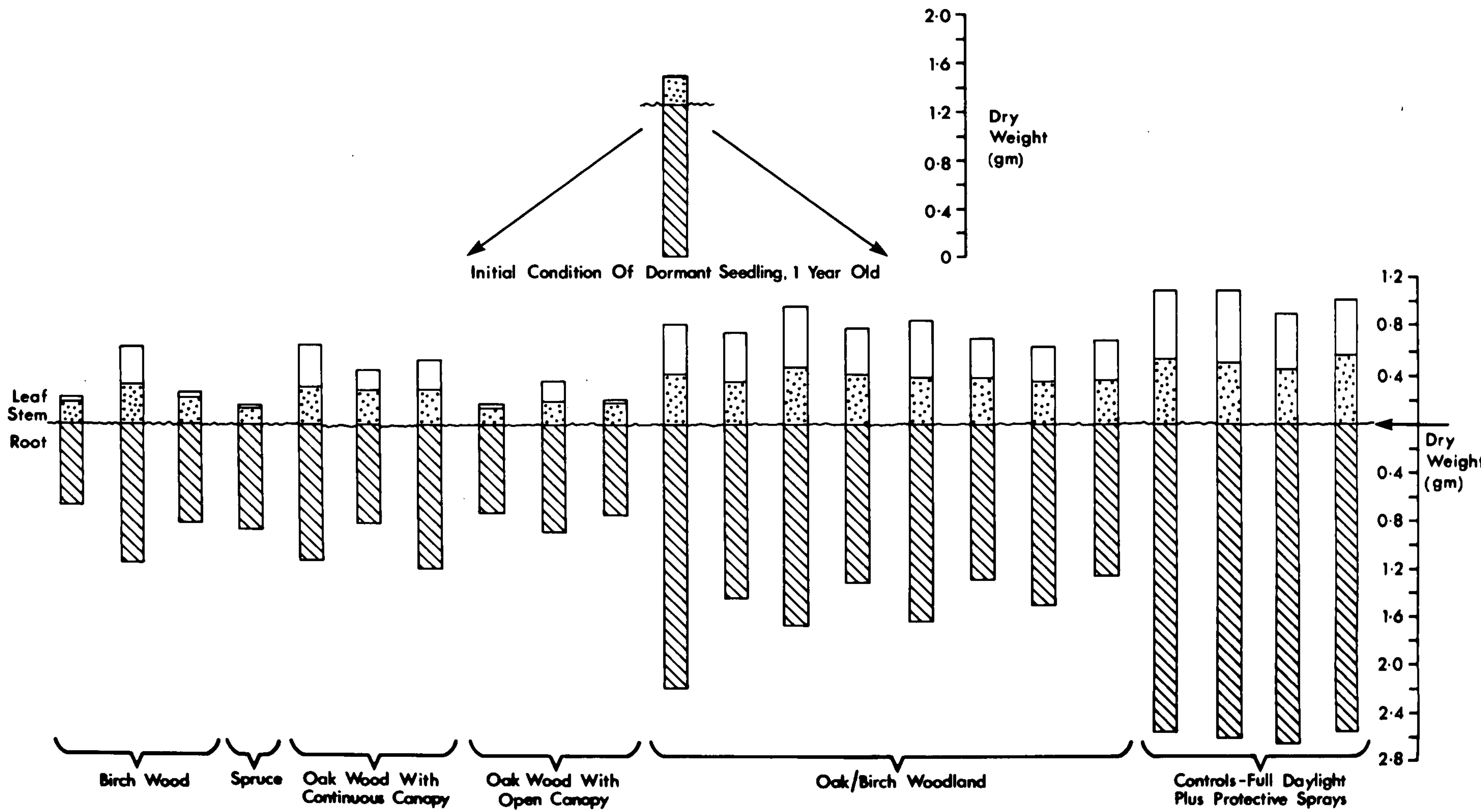
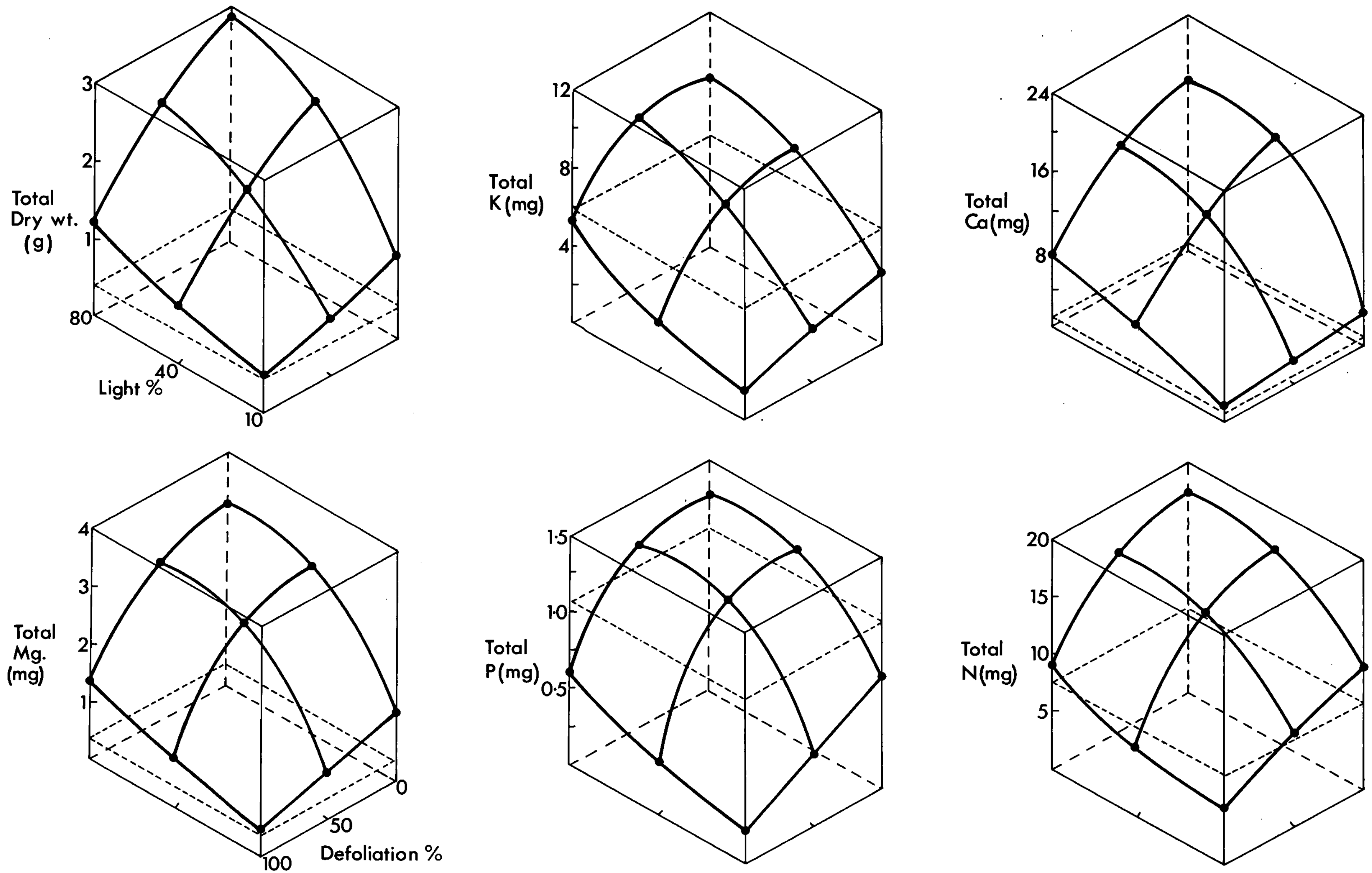


Fig. 10 *The effect on dry weight accumulation of exposing oak seedlings during their second year to different woodland conditions. For details of canopy conditions see Table 8: Saplings harvested in October.*



--------- = COMPENSATION POINT IN RELATION TO ACORN

Fig. 11 *Two year cumulative effects of defoliation and different light intensities on total dry weights of oak seedlings and their accumulations of potassium, calcium, magnesium, phosphorus and nitrogen. / Reproduced by kind permission of the publishers of "The British Oak" edited by Morris, M.G. and Perring, F.H. 1974. Faringdon, Classey.*

most young oak trees, up to *c* 5ft (150 cm) are heavily browsed. Only a minority, growing in large clearings with virtually full daylight, seem able to withstand this pressure.

1. Experimental

In the absence of grazing, or where numbers of animals are carefully controlled, the effects of tree canopy become increasingly important. The amount of light penetrating to the forest floor has an obvious influence on seedling growth and it is not difficult to determine the direct effect of this factor (see Jarvis, 1964; Ovington & MacRae, 1960). However, the presence of a tree canopy brings other problems to tree seedlings in the form of defoliating caterpillars, other invertebrates and fungi. Some of the effects of defoliating caterpillars can be measured by subjecting test oak seedlings (in pots) to various situations in a woodland. Table 8 shows the effect on leaf area and numbers of leaves/plant of a range of woodland conditions when compared with controls. The effect on leaf area is even more drastic than is indicated by the full daylight controls because oak seedlings in shade normally produce a larger leaf area in response to shade (an additional 10% under 50% daylight and 25% under 10% daylight). The cumulative effect on dry weight production of the different conditions to which the same seedlings were subjected is shown in Figure 10. There is a good deal of variability in these results, some of which defies simple explanation. Indeed, much of the variation is due to such chance events as whether a canopy tree in the immediate vicinity carried a large or small population of caterpillars in the year in question.

In more carefully controlled experimental conditions, pot-grown oak seedlings were subject to 3 different intensities of light (90%, 45% and 10% of full daylight) and 3 amounts of defoliation (0%, 50% and 100%, inflicted by cutting leaves) (see also Shaw, 1974). Effects of these treatments on dry weight accumulation and the reserves (amount/seedling) of different nutrients are shown in Figure 11. In terms of compensation point, as compared with what was contained in the original acorn, phosphorus uptake is clearly the most important factor. Potassium and nitrogen uptake can also be regarded as rather marginal for satisfactory growth. These experimental seedlings were protected against other "adverse influences", such as oak mildew and aphids, which are likely to affect most seedlings in woodland conditions. Because of this protection, the results probably overestimate seedling performance in the field but again the effect of root restriction in a pot and the absence of competing vegetation are unknown.

2. Discussion

As the above results demonstrate, the reduction of leaf area in oak seedlings has a large effect on their performance. This effect has 3 main sources (a) direct loss of material to the caterpillars, (b) impaired ability to photosynthesise during June and July and (c) the need to produce new leaves

TABLE 8 Effects of different environments on the leaf development (number and total leaf area) of pot-grown oak seedlings. Assessments made on 3 occasions. Ranges of replicates given in brackets.

		Nos. of replicates	Leaf areas (cm^2)			Leaf numbers		
			2 JULY	12 SEPT.	20 OCT.	2 JULY	12 SEPT.	20 OCT.
I	Growing in full daylight and protected with fungicidal and insecticidal sprays	4	63 *(55-67)*	78 *(65-89)*	74 *(64-84)*	8.7 *(7.5-9.7)*	12.6 *(10.3-14.8)*	12.3 *(10.2-14.2)*
II	Growing in birch wood	3	20 *(11-27)*	38 *(22-63)*	32 *(16-58)*	5 *(4.9-5.6)*	8 *(5.4-11.4)*	7 *(4.9-10.6)*
III	Growing in stand of spruce	1	2 *(–)*	5 *(–)*	5 *(–)*	2.1 *(–)*	4.8 *(–)*	1.6 *(–)*
IV	Growing in oak wood with continuous canopy	3	16 *(5-25)*	70 *(43-73)*	59 *(41-76)*	5.6 *(2.5-7.5)*	10.8 *(8.9-12.4)*	9.4 *(7.7-11.0)*
V	Growing in oak wood with open canopy	3	8 *(3-13)*	10 *(5-16)*	8 *(5-15)*	3.7 *(2.6-4.4)*	3.0 *(2.4-3.5)*	2.6 *(2.0-3.2)*
VI	Growing in oak/birch woodland	8	32 *(20-44)*	67 *(46-95)*	61 *(48-93)*	8.5 *(6.8-9.9)*	14.3 *(9.6-16.0)*	12.1 *(9.4-15.5)*

(which they do quite successfully), the use of which is restricted to about half the growing season before they are shed in the autumn. Interestingly, removal of the whole shoot system of an oak seedling at ground level in the dormant season (simulated winter browsing) has rather less effect on dry weight accumulation than 100% defoliation in May or June. The "browsed" seedling merely flushes a bud at ground level and produces a shoot system with no delay in the spring. The leaves on this shoot can then be used for the full growing season and more than compensate for the larger loss of dry matter compared with defoliation. The high root/shoot ratio typical of oak seedlings (up to 10/1 in full daylight), in which the main weight is contained in a swollen tap root, is seen as an adaptation to resist the effects of browsing.

Less is known about other factors affecting the growth of oak seedlings, in particular the effects of different amounts of soil nutrients and competition with the ground layer vegetation. Preliminary experiments with fertilizers suggest that they may only serve to intensify competition with ground-layer species (*Deschampsia flexuosa* in particular in north Wales). A reduction in root competition produced by excising all roots entering an area produces quite a marked increase in the growth of oak seedlings within this area. The main effect would seem to be through the cutting of tree roots. The effects of mycorrhizas on oaks are unknown but are suspected to be important.

Clearly some further information is required before a satisfactory model of oak regeneration could be constructed and it is a still bigger jump to understanding woodland regeneration in which a number of species are competing. It may also be important to understand the performance of individual seedlings rather than work in terms of the mean seedling. Oak seedlings seem to be particularly variable in their growth strategy eg date of flushing, length of shoot produced and whether they indulge in lammas growth or not. For example, pot-grown seedlings, 2 years old can have root/shoot ratios that vary from as little as 2/1 to 10/1 and flushing dates can vary by as much as 6 weeks from first to last. In the field, seedlings behave with similar variability and this variation may explain why the occasional seedling survives and continues to make slow growth long after others have died. Extreme physiological variation and selection may be an important factor in the success of oak as a widespread tree in British woodlands.

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