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Jonathan Silvertown

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LEAF-CANOPY-INDUCED SEED DORMANCY IN A GRASSLAND FLORA

By JONATHAN SILVERTOWN*

School of Biology, University of Sussex, Falmer, Brighton, Sussex, BN1 9QG, U.K.

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SUMMARY

The germination of 27 species from calcareous grassland was tested in three light treatments in the laboratory: in darkness, under tungsten lamps and under a leaf-canopy. Germination was significantly lower under a leaf-canopy than in the dark in 17 species. The phenomena of leaf-canopy induced dormancy was not associated with the life-span of species, though there was a weak, negative relationship with seed weight amongst 20 perennials in the sample. It is suggested that the co-existence of species at high density in calcareous grasslands may, in part, be explained by differences in germination response to fine-grained variations in the light environment at the soil surface.

INTRODUCTION

It has been argued by Harper *et al.* (1961), Harper, Williams and Sagar (1965) and Silvertown (1979) that the number of plants established from seed may be regulated by the availability of 'safe' germination sites and that inter-specific differences in germination requirements may be an important factor in allowing the co-existence of plant species in what appears to be a homogeneous habitat. One of the critical features of a 'safe site' is undoubtedly the correct degree and quality of illumination, with some buried seeds requiring only the briefest flash of light in order to break dormancy (Wesson and Wareing, 1968a, b) and other species requiring a specific photoperiod (Black and Wareing, 1954; Cumming, 1963).

'Gap detection' is the term coined by Thompson, Grime and Mason (1977) to describe the function of mechanisms which enable a seed to avoid germination until conditions are favourable for seedling survival. The most direct means of 'gap detection' for a seed would probably involve a mechanism sensitive to the degree of shading which the seedling would encounter if the seed were to germinate. The inhibitory effect of a leaf-canopy on seed germination provides just such a mechanism. Despite the numerous reports of such a phenomenon in the literature (e.g. Hannay, 1967; Black, 1969; Taylorson and Borthwick, 1969; King, 1975) there appears to be no systematic studies of sympatric species, as have been carried out by Thompson (1977) on the effect of fluctuating temperature on germination and Grime and Jarvis (1976) for light intensity (as distinct from light quality). King (1975) reported that the germination of three annual species, restricted to active ant hills in calcareous grassland, was inhibited by a leaf canopy and suggested this was an explanation for their absence from 'closed' chalk turf. Until now, however, the species of 'closed' turf themselves have not been systematically tested for the effect of a leaf canopy on germination.

* Present address: Department of Biology, Open University, Walton Hall, Milton Keynes, Buckinghamshire, U.K.

Calcareous grassland in Britain is typically a species-rich habitat in which plant species densities of up to 30 species per square metre are not uncommon. The co-existence of large numbers of species in these grasslands, which lack any apparent physical or topographical heterogeneity corresponding to the floristic diversity, presents a challenge to our understanding of niche separation in plants (Silvertown, 1979). There are local variations in leaf area index (Dickie, 1977). Thus plants themselves may contribute to the heterogeneity of the habitat by producing small scale variation in the spectral composition of the light reaching the soil surface. Micro-variations in spectral composition are therefore of potential importance in allowing the co-existence of sympatric species which have different germination responses.

This paper examines the germination response of 27 species of calcareous grassland in laboratory conditions designed to simulate the effect of a leaf canopy on seed germination in the field. Field experiments on a subset of these species will be reported elsewhere (Silvertown and Wilkin, in preparation).

The present experiments were designed to test whether seeds which germinate equally well in the dark and in the light, would do so in the light regime present under a canopy of leaves. Where the induction of dormancy was observed in seeds placed under a leaf canopy, the persistence of the dormant state when these seeds were transferred to the dark was also examined. This second test was designed to simulate the situation in which a seed with dormancy, induced in the field by a leaf canopy, subsequently became buried in the soil without any intervening period of exposure to full daylight. In effect, this is a test for the induction of a light requirement for germination caused by the leaf canopy.

MATERIALS AND METHODS

The inhibitory effect of light filtered through leaves on germination is a result of a decrease in the red/far-red ratio in the transmitted light affecting the phytochrome system of imbibed seeds (Smith, 1973). Black (1969) gives a transmission spectrum for leaves of *Tilia × europaea* L.* showing that transmission peaks at 720 nm and Dickie (1977) has shown that the transmission spectra of *T. europaea* and the common chalk grassland dominant *Zerna erecta* (Huds.) S. F. Gray are similar in this respect. *Tilia* leaves therefore provide a suitable filter and were used in the experiments described below. Tungsten light bulbs were used as a substitute for natural daylight since they provide an approximately equivalent ratio of red/far-red with greater reliability than can be obtained without artificial lighting.

The seed of 27 chalk grassland species collected in 1976 from Castle Hill National Nature Reserve, Sussex (TQ 365072) were used in the experiments (Table 1). Seeds were stored in the dark at room temperature in glass tubes closed with tight-fitting corks and sown (50 per dish) on a substrate of one per cent minimal agar in Petri dishes of 9 cm or 5 cm diameter. Germination was studied in three treatments, (a) in the dark (lids covered with two layers of aluminium foil); (b) under a leaf canopy (lids covered with two layers of *Tilia* leaves) and (c) in the light (lids left uncovered). The bottom and sides of all dishes were covered with two layers of aluminium foil.

All experiments were carried out in a culture room with a 12 h 'day' at 20 °C under illumination from 9 × 60 W tungsten bulbs suspended 1 m above the treatments. The lids of leaf treatments were replaced every 4 days with a covering of fresh leaves

* Nomenclature follows Clapham, Tutin and Warburg (1962).

without exposing the dishes to light. Where it was suspected that some results may have been affected by the ageing of leaves used in a treatment and when no fresh *Tilia* leaves were available, the experiment was repeated for four species using far-red 'Cinemoid' filters (Hannay, 1967, see table 3).

It was thought that CO₂ 'narcosis' (Kidd, 1914) might account for some inconsistent results in preliminary experiments and a comparison of germination in dishes sealed with paraffin film and in unsealed dishes was made. No significant effects were found; however, where the accurate counting of seeds in light treatments required a lid to be removed the lids of other treatments were also removed briefly in the dark to prevent, as far as possible, any differences in atmospheric conditions occurring between treatments.

The replication of treatments was designed to reduce disturbance to the experiments caused by inspection of the dishes. Preliminary experiments during which dishes with leaf-canopy and dark treatments were opened under a weak green light to count germinated seed suggested that this procedure stimulated germination. Baskin and Baskin (1979) have also reported that the light from a green safe lamp may affect seed germination. A procedure designed to overcome this problem required the following number of replicates per species: light (2), dark (4), leaf-canopy (4). The experimental design is shown in Figure 1.

The progress of germination in the light treatments was followed from the beginning of the experiment and when germination in this treatment reached completion (a constant count on three successive occasions) the lids of two dark treatments and of two leaf treatments were removed and germination counts made. In species where significantly fewer seeds germinated under leaves than in the dark replicates, R1 and R2 (Fig. 1) were continued in a further stage of the experiment. The lids of the two intact leaf replicates (R2) were fitted with dark lids and germination in the replicates transferred from leaves to light was followed to completion. At completion, replicates R1 and R2 were opened and counted. Where germination in R2 was still significantly less than in other treatments the dishes were maintained in the light until germination had reached completion.

This experimental design allows germination under a leaf canopy to be compared with that in the dark and in the light. It also makes it possible to detect any light requirement induced in seeds by the leaf treatment from a comparison of germination following the transfer of two leaf treatments to the light and the two transferred to the dark.

Statistical treatment of results

A non-parametric, two-way *G* test (Sokal and Rohlf, 1969) was used to compare replicates and pairs of treatments. The treatments tested for significant differences were:

light \times dark,
leaf canopy \times dark,
leaf canopy to dark \times leaves to light.

A comparison of light and leaf canopy treatments would have involved two variables: light intensity and red/far red ratio. No comparison of these treatments was made because it would not produce an unambiguous indication of which of the two factors was responsible for any induced dormancy. Consequently a light \times dark comparison was made to test for any light intensity requirement in seeds and a leaf

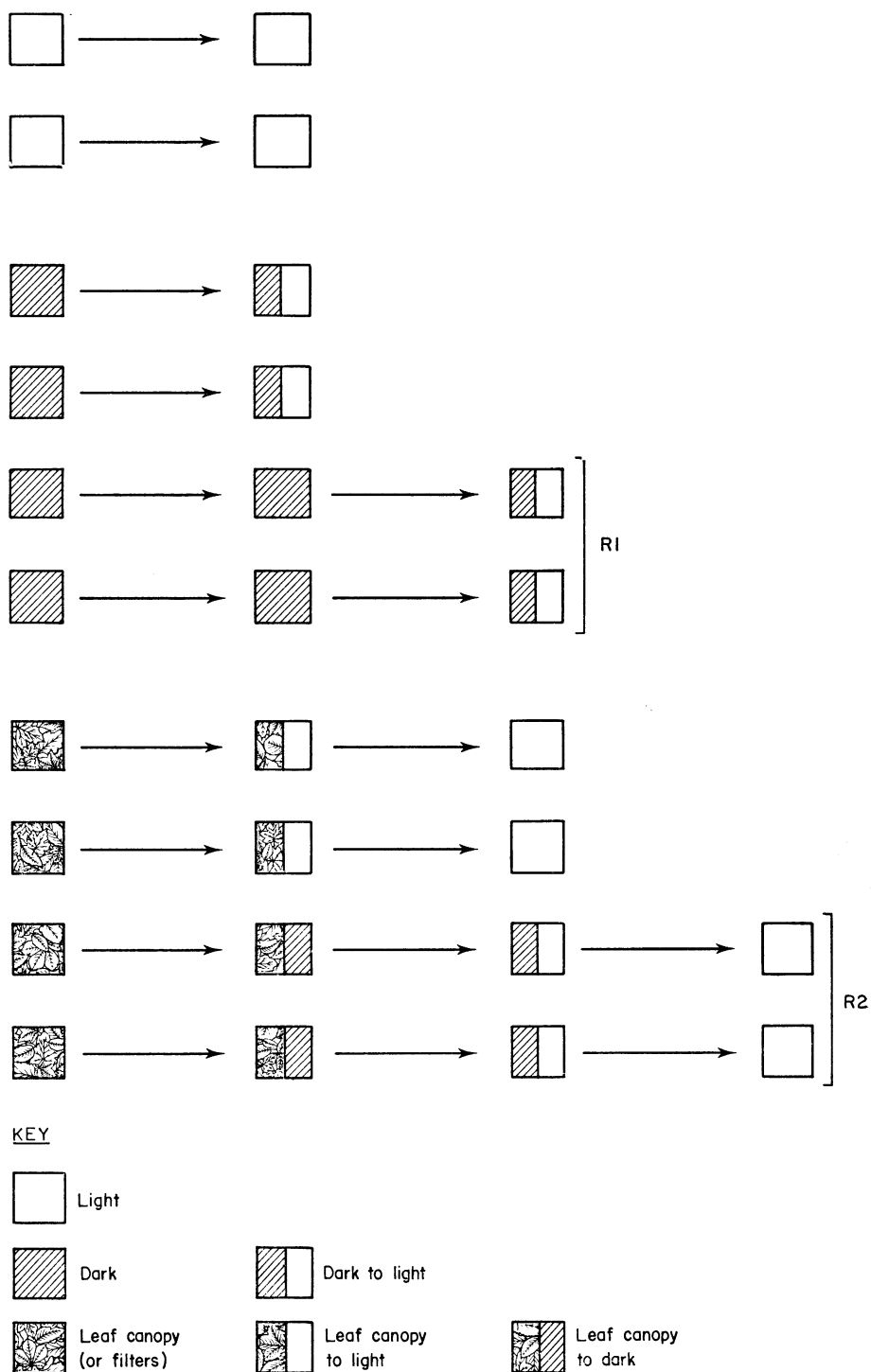


Fig. 1. The experimental design used to test seeds for the occurrence of leaf-canopy-induced seed dormancy. See text for details.

canopy \times dark comparison was used to test for leaf canopy induced dormancy in species which showed no light intensity requirement in the first test.

Leaf canopy induced dormancy was defined as:

$$\% \text{ leaf canopy induced dormancy} = 100 \times \frac{N_d - N_{lf}}{N_d}$$

where N_d = number of seeds germinating in dark treatments, and N_{lf} = number of seeds germinating in leaf-canopy treatments.

For the purposes of further analysis species were divided into two lifespan categories (annual + biennial and perennial). Tests of association between lifespan category and induced dormancy and seed weight and induced dormancy were made, treating induced dormancy as a discrete, binary variable. A comparison of the number of species exhibiting induced dormancy in each life-span category would be valid only if variation in seed germinability (percentage germination in dark treatments) was the same in each group. This condition was tested by a two-tailed Mann-Whitney U -test (Seigal, 1956). Valid cross-species correlations of ecological variables also require phylogenetic constraints to be taken into account since these may be a source of spurious correlation between a set of characters if these are shared in common by all species in a taxon (Clutton-Brock and Harvey, 1977). Consequently, families in which all species share the same germination response must be treated as the equivalent of a single species. This rule was applied to species in the Caryophyllaceae Leguminosae, Plantaginaceae and Labiatae for the purpose of comparing life-span and induced dormancy. A G -test was used to compare the relative occurrence of induced dormancy amongst the appropriate taxa in the two life-span categories.

Spearman Rank Correlation was used as a test of association between seed weight and induced dormancy within life-span categories. Since seed weight is a continuous variable, species in the Caryophyllaceae, Leguminosae, Plantaginaceae and Labiatae were treated as independent points for this test. The consequences of this are discussed below.

RESULTS AND DISCUSSION

Leaf-canopy-induced dormancy and life-span

There was no statistically significant difference in the germinability of annual/biennial and perennial species ($P < 0.10$, Mann-Whitney U -test). Of the seven annual or biennial species tested, six showed more than 25% leaf induced dormancy (Table 1). There is no clear reason why *Centaureum erythraea* was the exceptional species amongst these plants, especially since *Blackstonia perfoliata*, a species with close ecological and taxonomic affinities with *C. erythraea* showed strong leaf-induced dormancy (85%). The experiment using *C. erythraea*, was repeated three times and each time produced the same result, suggesting that germination response under a leaf canopy may be a reliable and ecologically important difference between the regeneration habits of *Centaureum* and *Blackstonia*.

The sample of 20 perennial species tested contained 11 species in which some leaf-induced dormancy was detected, this ranged from 20 to 78% (Table 1). On the basis of the phylogenetic rule mentioned above, these 20 species were divided into nine independent cases of induced dormancy and six of non-dormancy (Table 2). No significant difference in dormancy between the two life-span categories was found ($G = 1.59$, $P > 0.05$). Indeed, there is no obvious advantage which should accrue to

an annual or biennial species exhibiting leaf-induced dormancy which would not also benefit a perennial of the same seed size.

Leaf-canopy-induced dormancy and seed weight

The sensitivity of a seed to its microenvironment may be expected to increase as the seed size of a species diminishes. Small seeds, having smaller stored food resources than large ones, produce seedlings which must become entirely dependent upon

Table 1. *The occurrence of leaf-canopy induced dormancy in 27 species of the chalk grassland flora. Species are listed in descending order of seed weight, within the two life-span categories annual + biennial and perennial*

| Family | Annual and biennials | Induced dormancy (%) | P difference from dark control | Germination in dark control (%) |
|------------|--|----------------------|--------------------------------|---------------------------------|
| Annuals | | | | |
| COMP | <i>Carlina vulgaris</i> L. | 72 | *** | 50 |
| UMB++ | <i>Daucus carota</i> L. | 27 | ** | 35 |
| CARO | <i>Cerastium holosteoides</i> Fr. | 92 | *** | 100 |
| CRU | <i>Arabis hirsuta</i> (L.) Scop. | 35 | *** | 100 |
| GENT | <i>Centaurium erythraea</i> Rafn. | 0 | — | 74 |
| GENT | <i>Blackstonia perfoliata</i> (L.) Huds. | 85 | *** | 88 |
| CARO | <i>Arenaria serpyllifolia</i> L. | 57 | *** | 59 |
| Perennials | | | | |
| LEG | <i>Onobrychis viciifolia</i> Scop. | 0 | — | 88 |
| COMP | <i>Centaurea scabiosa</i> L. | 0 | — | 21 |
| LEG | <i>Ononis repens</i> L. | 0 | — | 16 |
| COMP+ | <i>Cirsium acaulon</i> (L.) Scop. | 0 | — | 17 |
| LEG | <i>Anthyllis vulneraria</i> L. | 0 | — | 42 |
| COMP | <i>Centauria nigra</i> L. | 30 | * | 63 |
| LAB++ | <i>Prunella vulgaris</i> L. | 78 | *** | 78 |
| PLAN+ | <i>Plantago lanceolata</i> L. | 27 | * | 54 |
| LEG+ | <i>Lotus corniculatus</i> L. | 0 | — | 36 |
| POLY | <i>Rumex acetosa</i> L. | 60 | *** | 62 |
| COMP+ | <i>Leontodon hispidus</i> L. | 40 | *** | 60 |
| ROS | <i>Filipendula vulgaris</i> Moench. | 0 | — | 38 |
| PLAN | <i>Plantago media</i> L. | 33 | *** | 86 |
| CARO | <i>Silene nutans</i> L. | 0 | — | 76 |
| COMP++ | <i>Chrysanthemum leucanthemum</i> L. | 49 | *** | 63 |
| RUB | <i>Galium verum</i> L. | 52 | *** | 70 |
| COMP | <i>Hieracium pilosella</i> L. | 0 | — | 72 |
| HYP | <i>Hypericum perforatum</i> L. | 30 | *** | 84 |
| COMP | <i>Achillea millefolium</i> L. | 70 | *** | 100 |
| LAB | <i>Origanum vulgare</i> L. | 20 | *** | 100 |

+ = Species tested under a far-red filter only. ++ = Similar result obtained from an experiment using a far-red filter. P = significance level using a two-way G-test (see text).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The families are indicated by abbreviations of the following: Caryophyllaceae, Compositae, Cruciferae, Gentianaceae, Hypericaceae, Labiatae, Leguminosae, Plantaginaceae, Polygonaceae, Rosaceae, Rubiaceae, Umbelliferae.

photosynthesis earlier or at a smaller size than large seeded species meeting the same problems of interference or competition. The importance of locating the correct moment for germination is therefore likely to become an increasingly critical factor in the survival of seedlings as seed size decreases.

Species have been ranked by seed weight within each life-span category in Table 1.

No association of seed weight and leaf-induced dormancy was detected in the annual/biennial group though such a relationship did occur amongst the perennials ($P < 0.05$). The Spearman Rank Correlation coefficient for this association $R_s = 0.43$, was corrected for tied values. The occurrence of more than five species with zero dormancy near the top of the table was responsible for the relationship between dormancy and seed weight. There is no relationship between seed weight and percent dormancy within the subset of 11 perennial species for which percentage dormancy is greater than zero (Spearman Rank Correlation, $R_s = 0.04$). One must therefore conclude that no unambiguous relationship between seed weight and leaf-induced dormancy is shown by these data with the qualification that the germination of the heaviest seeded species does tend to be insensitive to the presence of a leaf canopy.

Table 2. *The number of taxa showing leaf-canopy-induced seed dormancy by life-span. Species in the same family, exhibiting the same germination response have been treated as a single case*

| | Leaf-canopy- induced dormancy | No leaf-canopy- induced dormancy |
|---------------------|----------------------------------|-------------------------------------|
| Annuals + biennials | 5 | 1 |
| Perennials | 9 | 6 |
| Total | 14 | 7 |

The degree of leaf-induced dormancy amongst smaller seeded species must be determined by ecological parameters more diverse than those of seed weight and life-span which have been considered here. The colour of the seed coat and its permeability to far-red light will be factors determining whether a species may employ this means of gap detection. The seeds of *Hieracium pilosella* and *Silene nutans* both have black testas which is perhaps the reason that they do not exhibit leaf-induced dormancy despite their small size. One may speculate that the characteristically hard seed coat of the Leguminosae may also constrain the evolution of any gap-detecting mechanism involving far-red though these species are also relatively heavy-seeded and may consequently not experience strong selection in favour of such a mechanism. Polymorphism in the response of seeds to far-red may be expected and far-red sensitivity may be linked to other germination characters. This factor complicates the interpretation of results obtained in germination experiments where the total percentage of seeds germinating is low. It is not known in such circumstances whether the ungerminated seeds also exhibit leaf-induced dormancy. 100% leaf-canopy induced dormancy was not observed in any species. Individual seeds within a population clearly vary in their response to a leaf-canopy and the proportion of germinable seeds showing induced dormancy also varies between species. Cohen (1966) has shown that the ratio of dormant to non-dormant seeds produced by a hypothetical annual plant should be directly proportional to the risk of reproductive failure for the progeny. Innate dormancy mechanisms (sensu Harper, 1977) allow less flexibility in the adjustment of the dormant/non-dormant seed ratio to the currently prevailing risk of germinating than do induced dormancy mechanisms. Such flexibility should be less important where death risks are higher in post-seedling phases of the life-history than in the seed-to-seedling phase, unless germination conditions and subsequent successful

reproduction are related. There is evidence that this may be the case for *Daucus carota* (Holt, 1972; Silvertown, 1979). Several aspects of a species life-history may therefore determine the selection pressures operating in favour of any gap-detecting mechanism.

The induction of a germination light requirement by a leaf canopy

No species exhibiting leaf-canopy-induced dormancy was shown to have acquired a light requirement for germination. Seeds must therefore rely upon an independent mechanism of dormancy induction when they enter the soil beneath a leaf canopy if they are not to germinate.

The results of Wesson and Wareing (1968b), which show that burial of seed in soil induces dormancy, may be seen as a complementary adaptation to leaf-induced dormancy. The former mechanism will ensure that a seed resting on the soil surface which delays germination because of the presence of a leaf canopy will not suddenly germinate if it enters the darkness of the soil unless there is positive evidence (i.e. light) that a leaf canopy is no longer present.

Table 3. *Red/far-red ratios for the transmission of light through various types of experimental and natural leaf canopy*

| Type of leaf canopy | Ratio of red/far red | Source |
|--------------------------------------|----------------------|---|
| Above a <i>Zerna</i> tussock | 1.2 | Dickie (1977) |
| Shaded bare ground | 0.85 | |
| Moderate shade, edge of tussock | 0.80 | |
| Very deep shade, middle of tussock | 0.67 | |
| <i>Zerna</i> leaves (2 layers) | 0.20 | |
| <i>Tilia</i> leaves (2 layers) | 0.25 | Taylorson and Borthwick (1969) Hannay (1967) |
| <i>Nicotiniana</i> leaves (2 layers) | 0.28 | |
| 'Cinemoid' filters | < 0.10 | |

Leaf-canopy-induced dormancy and partitioning of the grassland habitat

Measurements of the red/far-red ratio in germination micro-sites in the field (Wilkin and Silvertown, in prep.) are necessary in order to demonstrate positively whether this kind of induced dormancy is of likely importance to species in their partitioning of the habitat on a micro-scale. Some indicative measurements of the red/far-red ratio beneath and near clumps of *Zerna erecta* in chalk grassland have been reported by Dickie (1977) and are reproduced with his permission in Table 3.

Given that there is fine-grained spatial variation in the spectral composition of the light penetrating the leaf canopy in grasslands, and that seeds are responsive to this variation, it is still necessary to establish some further conditions before the ecological significance of these phenomena are established. The co-existence of species due to the partitioning of the habitat in the 'regeneration niche' (sensu Grubb, 1977) through different germination responses requires that population size is regulated by the number of unique 'safe' germination sites available.

This condition is most likely to be met in species reproducing predominantly by seed such as the two annuals *Blackstonia perfoliata* which showed 80% induced dormancy in experiments, and *Centaureum erythraea* which showed none. These results suggest that *B. perfoliata* could not germinate in shaded conditions where *C. erythraea* could readily become established. Overlap of *C. erythraea* on to niche-

space of *B. perfoliata* may be limited by some other factor in the regeneration of the two species which prevents the former species displacing *B. perfoliata* in unshaded micro-sites. The different germination responses of these two closely related and sympatric annuals demonstrates the potential ecological significance of leaf-induced dormancy in the maintenance of species diversity in grassland.

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REFERENCES

- BASKIN, J. M. & BASKIN, C. C. (1979). Promotion of germination of *Stellaria media* seeds by light from a green safe lamp. *New Phytologist*, **82**, 381–383.
- BLACK, M. (1969). Light-controlled germination of seeds. *Symposium of the Society of Experimental Biology*, **23**, 193–217.
- BLACK, M. & WAREING, P. F. (1954). Photoperiodic control of germination in seed of birch (*Betula pubescens* Ehrh.). *Nature*, **174**, 705.
- CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. (1962). *Flora of the British Isles*, 2nd edn. Cambridge.
- CLUTTON-BROCK, T. H. & HARVEY, P. H. (1977). Primate ecology and social organization. *Journal of Zoology, London*, **183**, 1–39.
- COHEN, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, **12**, 119–129.
- CUMMING, B. G. (1963). The dependence of germination on photo-period, light quality and temperature in *Chenopodium* spp. *Canadian Journal of Botany*, **41**, 1211–1233.
- DICKIE, J. B. (1977). The reproduction and regeneration of some chalk grassland perennials. Ph.D. Thesis, University of Cambridge.
- GRIME, J. P. & JARVIS, B. C. (1976). Shade avoidance and shade tolerance in flowering plants. II. Effects of light on the germination of species of contrasted ecology. In: *Light as an Ecological Factor*, vol. II (Ed. by G. C. Evans, R. Bainbridge & O. Rackham), pp. 525–535. Oxford: Blackwell.
- GRUBB, P. J. (1977). The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- HANNAY, J. W. (1967). Light and seed germination – an experimental approach to photobiology. *Journal of Biology Education*, **1**, 65–73.
- HARPER, J. L. (1977). *The Population Biology of Plants*. London.
- HARPER, J. L., CLATWORTHY, J. N., McNAUGHTON, I. H. & SAGAR, G. R. (1961). The evolution of closely related species living in the same area. *Evolution*, **15**, 209–227.
- HARPER, J. L., WILLIAMS, J. T. & SAGAR, G. R. (1965). The behaviour of seeds in the soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of Ecology*, **53**, 273–286.
- HOLT, B. R. (1972). The effect of arrival time on recruitment, mortality and reproduction in successional plant populations. *Ecology*, **53**, 668–673.
- KIDD, F. (1914). The controlling influence of carbon dioxide in the maturation, dormancy and germination of seeds. *Proceedings of the Royal Society, B*, **87**, pp. 408–421, 609–625.
- KING, T. J. (1975). Inhibition of seed germination under leaf canopies in *Arenaria serpyllifolia*, *Veronica arvensis* and *Cerastium holosteoides*. *New Phytologist*, **75**, 870–90.
- SEIGAL, S. (1956). *Non-parametric Statistics for the Behavioural Sciences*. Ames.
- SILVERTOWN, J. W. (1979). The maintenance of species diversity in grassland, with particular reference to chalk grassland. D.Phil. Thesis, University of Sussex.
- SMITH, H. (1973). Light quality and germination: ecological implications. In: *Seed Ecology* (Ed. by W. Heydecker). London.
- SOKAL, R. R. & ROHLF, F. J. (1969). *Biometry*. San Francisco.
- TAYLORSON, R. B. & BORTHWICK, H. A. (1969). Light filtration by foliar canopies: significance for light controlled weed seed germination. *Weed Science*, **17**, 48–51.
- THOMPSON, K. (1977). An ecological investigation of germination responses to diurnal fluctuations in temperature. Ph.D. Thesis, University of Sheffield.

- THOMPSON, G., GRIME, J. P. & MASON, G. (1977). Seed germination in response to diurnal fluctuations in temperature. *Nature*, **267**, 147–149.
- WESSON, G. & WAREING, P. F. (1969a). The role of light in the germination of naturally occurring populations of buried weeds. *Journal of Experimental Botany*, **20**, 402–413.
- WESSON, G. & WAREING, P. F. (1969b). The induction of light sensitivity in weed seeds by burial. *Journal of Experimental Botany*, **20**, 414–425.