Large-seeded species are less dependent on light for germination than small-seeded ones

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Abstract

Germination in light and darkness was compared after cold stratification of seeds of 54 species known or suspected to accumulate persistent seed banks. Germination became less dependent on light with increasing seed mass. This pattern was clear in a direct correlation of individual species data (P <0.0001) as well as when considering phylogenetically independent contrasts (P <0.001). The latter analysis suggests that light response and seed mass coevolved.

Keywords: evolution, germination, light, phylogenetic correction, seed size, stratification, Sweden.

Introduction

A light requirement for germination is one of the main determinants of the ability of species to accumulate a persistent soil seed bank (e.g. Baskin and Baskin, 1989; Pons, 1991; Milberg, 1994). Seeds of some species have an initial light requirement for germination (Grime *et al*., 1981; Baskin and Baskin, 1988), while those of other species seem to acquire a light requirement only after burial in the soil (Wesson and Wareing, 1969; Scopel, *et al*., 1991; Derkx and Karssen, 1993; Noronha *et al*., 1997).

Light can penetrate only a few millimetres in soil (Kasperbauer and Hunt, 1988; Mandoli *et al*., 1990; Benvenuti, 1995; Cussans *et al*., 1996). Hence, seeds could use absence of light to indicate burial at some depth while light would indicate location on or near the soil surface. However, seedlings from large seeds can emerge successfully from much greater depth than light can penetrate (e.g. del Arco *et al*., 1995). Therefore, light would not be an appropriate germination cue for such species. Consequently, when comparing species whose seeds can accumulate in the soil, small-seeded species are expected to have a light requirement for germination, while germination in large-seeded ones might be expected to be indifferent to light. Such a pattern was, in fact, detected by Grime *et al*. (1981), but that study included light responses of non-stratified seeds, which is less relevant in a field situation (most species do not germinate immediately after being shed, but after spending some time on or in the soil). Further, that study also included numerous species lacking the ability to persist in the soil, and a light cue for germination seems less relevant for seeds that cannot survive in the soil. However, it must be remembered that persistence in the soil is itself strongly correlated with seed size (Thompson *et al*., 1993; Hodkinson *et al*., 1998) and that large-seeded species with persistent seed banks are relatively uncommon.

We investigated the light requirement for germination in cold-stratified seeds of 54 species, with different seed masses (0.032–22 mg), known or suspected to form persistent soil seed banks (Thompson *et al*., 1997; personal observations). The cold stratification simulated a winter and affects the dormancy level of seeds of most species (Milberg and Andersson, 1998) and can, in some species, induce a light requirement for germination (Noronha *et al*., 1997). Hence, the results reported here simulated the spring situation in a ruderal plant community, and it is important to note that the seed batches used differed in their dormancy level, with few being completely non-dormant. Therefore, we also tested the assumption that the proportion of seeds capable of germination in darkness is unaffected by dormancy level. Also worth noting is that although most species have physiological seed dormancy, a few possess physical dormancy. We looked for a direct relationship between seed mass and light requirement among the 54 species. However, since related species are likely to share similar attributes, such a test cannot explore evolutionary relationships. Therefore, we also looked for a relationship between phylogenetically

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https://doi.org/10.1017/S0960258500000118 Published online by Cambridge University Press

independent contrasts (Harvey and Pagel, 1991) to test if seed mass and light requirement have coevolved.

Materials and methods

Seeds of the 54 species included in this study (Table 1) were collected in August 1994 in southern Sweden. They represent typical species growing in farm land, horticultural fields and ruderal habitats that have ripe seeds available at that time of the year. For most species, seeds were collected from three sites (separated by >3 km) but in some cases from only two sites or one (one and six species, respectively). For other details on the germination of these 54 species, see Milberg *et al*. (1996) and Milberg and Andersson (1998), where some of the data presented here were reported in a different context.

Seeds were dried at room temperature (22 ± 2°C) for 10 days and stored for 2 months before the start of cold stratification. Batches of about 100 seeds (in some cases fewer owing to seed shortage, or more in species with minute seeds difficult to handle) were placed on filter paper (two Munktell 1003, 90 mm diameter) and wetted with de-ionised water (4.0 ml) in Petri-dishes (90 mm diameter). For each seed population, two dishes were sealed with parafilm, while two were immediately wrapped in aluminium foil. The dishes were then cold-stratified in complete darkness at 3 ± 0.5°C for 18 weeks (10–13 October 1994 to 10–15 February 1995; during which there was a 10-day period of about 11°C because of a power failure).

The germination experiment was conducted in a room with diurnally fluctuating temperature. The temperature was 3.5 ± 1.0°C for 9 h and 18.5 ± 2.0°C for 11 h, with transitions between these temperatures accounting for the other 4 h. This temperature regime corresponds with near-surface soil temperatures during the spring germination period in April and May in southern Sweden (Milberg and Andersson, 1997; unpublished data). Light exposure (12 h; PAR 10.5 ± 1.5 μmol m^{-2} s^{-1}; ratio R/FR 8) coincided with the period with the high temperature and was provided by cool white fluorescent tubes (OSRAM L65W/20R). Seeds germinated in the light treatment were counted and removed regularly, but the dishes wrapped in aluminium foil were not opened until the experiment was terminated. Three weeks after the start of the germination test, when germination in light had ceased (germination in light proceeded more slowly than in darkness under parallel conditions; Milberg, 1997), examination and termination of treatments started and lasted for about two weeks.

Germination percentages were recorded in light and in darkness, and based on viable seeds only, were used to calculate an index expressing a light requirement: Relative Light Germination (RLG)

$$RLG = Gl / (Gd + Gl) \quad (1)$$

where Gl = the germination percentage in light, and Gd = the germination percentage in darkness. We considered relative values preferable to germination percentages since seed batches differed in their dormancy level. RLG represents a range of values varying from 0 (germination only in darkness) to 1 (germination only in light). RLG was not calculated for seed populations where less than 10% of the seeds had germinated in light or in dark (to exclude RLG calculations based on few seeds). Hence, the number of RLG values calculated per species varied (1–3), and we used the average of these for further analyses.

Seed mass was determined for each seed population by weighing 20 batches of a known quantity of seed (often 100 seeds). We calculated an average seed mass for each species and used the log-transformed values in the analyses.

The linear regression between seed mass and RLG was analysed in two ways: with individual species data and by using phylogenetically independent contrasts. The latter analysis used a modified version of the CAIC (Comparative Analysis by Independent Contrasts) package (Purvis and Rambaut, 1995). CAIC calculates the difference (i.e. contrast) in the traits of interest between pairs of species. This contrast represents the amount of evolutionary divergence since the taxa speciated from their common ancestor. In addition, CAIC calculates contrasts at internal nodes of a phylogeny. Since we do not know what the ancestral species at these nodes were like, values at nodes are averages of the species (or nodes) that evolved from them. It is possible to weight these averages by the branch lengths, but in the present analysis we assumed that all branch lengths were equal. A dichotomous phylogeny with n species yields (n – 1) contrasts. In the present case, however, contrasts were fewer since we used a taxonomy that contained several polytomies. The important point is that each contrast is independent of all the others. A phylogeny based on molecular characters was used for higher taxonomic relationships between plant families (Chase *et al*., 1993) and within Asteraceae (Jansen *et al*., 1990). Phylogenetic relationships below the family level were otherwise approximated from Stace (1991). The null hypothesis states that seed mass contrasts and RLG contrasts are unrelated (i.e. no significant slope in a regression analysis of the contrasts). Put simply: evolutionary changes in seed mass are unrelated to changes in RLG. We tested this hypothesis by linear regression of standardised linear contrasts, forced through the origin [Purvis and Rambaut (1995) and Harvey and Pagel (1991) explain why the regression

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Table 1. Average germination in light, average relative light germination (RLG) and average seed mass for species included in the study. Nomenclature follows Tutin *et al*. (1964–1980)

	Germination in light %	RLG (n)	Seed mass (n) mg
Anchusa arvensis (L.) Bieb.	16	0.68 (1)	6.84 (3)
Apera spica-venti (L.) Beauv.	59	0.70 (2)	0.114 (3)
Avena fatua L.	14	0.47 (3)	22.2 (3)
Berteroa incana (L.) DC.	23	0.62 (1)	0.319 (1)
Bilderdykia convolvulus (L.) Dumort.	94	0.61 (3)	3.42 (3)
Buglossoides arvensis (L.) I.M. Johnston	88	0.60 (3)	6.28 (3)
Camelina microcarpa Andrz. ex DC.	11	0.51 (1)	0.300 (1)
Centaurea cyanus L.	91	0.59 (3)	4.04 (3)
Cerastium fontanum Baumg.	88	0.84 (1)	0.0837 (1)
Chaenorhinum minus (L.) Lange	82	0.77 (3)	0.0737 (3)
Chamomilla recutita (L.) Rauschert	58	1.00 (3)	0.0472 (3)
Chamomilla suaveolens (Pursh) Rydb.	75	0.97 (3)	0.109 (3)
Chenopodium album L.	75	0.97 (3)	0.614 (3)
Chenopodium polyspermum L.	75	0.85 (1)	0.211 (1)
Chenopodium suecicum J. Murr	52	0.97 (3)	0.598 (3)
Consolida regalis S.F. Gray	93	0.50 (3)	1.33 (3)
Conyza canadensis (L.) Cronq.	25	0.97 (2)	0.0320 (3)
Erodium cicutarium (L.) L'Hér.	16	0.47 (3)	2.22 (3)
Filaginella uliginosa (L.) Opiz	98	0.99 (3)	0.0345 (3)
Fumaria officinalis L.	14	0.54 (1)	3.66 (3)
Galeopsis bifida Boenn.	68	0.62 (2)	3.45 (3)
Galeopsis speciosa Miller	30	0.39 (3)	4.23 (3)
Galeopsis tetrahit L.	48	0.92 (1)	4.60 (3)
Galinsoga ciliata (Rafin.) S.F. Blake	99	0.98 (3)	0.215 (3)
Galium aparine L.	10	0.56 (1)	6.74 (3)
Lactuca serriola L.	99	0.66 (3)	0.533 (3)
Lamium amplexicaule L.	13	0.94 (3)	0.608 (3)
Lamium hybridum Vill.	87	0.58 (3)	1.10 (3)
Lamium purpureum L.	38	0.69 (2)	0.813 (2)
Lapsana communis L.	97	0.99 (3)	1.04 (3)
Matricaria perforata Mérat	99	0.97 (3)	0.290 (3)
Melilotus alba Medicus	33	0.57 (3)	1.65 (3)
Myosotis arvensis (L.) Hill	30	0.82 (2)	0.301 (3)
Poa annua L.	90	0.70 (3)	0.214 (3)
Polygonum aviculare L.	69	0.87 (3)	1.04 (3)
Polygonum lapathifolium L.	74	0.95 (3)	2.29 (3)
Polygonum persicaria L.	11	1.00 (1)	1.34 (1)
Rumex crispus L.	46	1.00 (3)	1.37 (3)
Rumex longifolius DC.	98	1.00 (3)	1.88 (3)
Rumex obtusifolius L.	94	1.00 (3)	1.27 (3)
Senecio vulgaris L.	92	0.96 (3)	0.162 (3)
Silene noctiflora L.	100	0.86 (3)	0.960 (3)
Sinapis arvensis L.	28	0.52 (3)	2.29 (3)
Sonchus asper (L.) Hill	99	0.85 (3)	0.414 (3)
Sonchus oleraceus L.	100	0.83 (3)	0.324 (3)
Spergula arvensis L.	21	0.58 (2)	0.374 (3)
Stellaria media (L.) Vill.	46	0.79 (3)	0.384 (3)
Taraxacum officinale group	100	0.63 (3)	0.378 (3)
Urtica urens L.	87	0.92 (3)	0.537 (3)
Verbascum thapsus L.	73	1.00 (2)	0.0875 (3)
Veronica agrestis L.	20	0.65 (2)	0.569 (3)
Veronica arvensis L.	49	1.00 (3)	0.108 (3)
Vicia hirsuta (L.) S.F. Gray	15	0.40 (1)	7.26 (1)
Viola arvensis Murray	14	0.56 (2)	0.681 (3)

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should be forced through the origin.]. Note that, in the present analysis, seed mass contrasts are ≥0. The RLG contrasts, however, can be either positive or negative, depending on whether they vary in the same or the opposite direction as seed mass. Hence, if increasing seed mass is associated with a decreasing light requirement, most of our RLG contrasts would be negative.

Results and Discussion

Although seed mass variation within a species is relatively small (Michaels *et al*., 1988; Fenner, 1992), RLG of a species is likely to vary phenotypically (e.g. Schütz and Milberg, 1997; Andersson and Milberg, 1998) and/or to depend on post-dispersal treatments seeds have experienced. More specifically, species with physiological dormancy can undergo seasonal changes in dormancy level, and, as a consequence, RLG might change somewhat seasonally (Milberg and Andersson, 1997). Still, one of our assumptions was that RLG was relatively unaffected by dormancy level, and this was supported by the highly significant correlations (R^2 = 0.5013, P <0.0001, n = 28 species) between the RLG values reported here and similar ones calculated for fresh seeds (unpublished data). Hence, although this study resembled a field situation in the spring, when species exhibit various degrees of seed dormancy (indicated by the various germination percentages noted in the light treatment in Table 1), we believe that the same type of pattern would emerge irrespective of time of the year. It is also worth stressing that it is difficult to capture the light response in a single variable like RLG. The response to light is a complex one that depends not only on the dormancy level of the seeds but also on the photon fluence, its spectral composition and the temperature regime under which germination is tested.

Among the studied species, RLG, i.e. the response to light, clearly decreased with seed mass (Fig. 1; $F_{(1, 52)}$ = 19.96, P <0.0001). Hence, our original hypothesis and the observations of Grime *et al*. (1981) were confirmed, suggesting that light as a germination cue becomes less important in species with relatively large seeds. Nevertheless, it is important to point out that RLG varies greatly (R^2 = 0.2774) and that a substantial amount of the variation is not accounted for by seed mass.

Six species germinated more or less equally well in light and darkness (RLG 0.45 – 0.55; *Avena fatua, Camelina microcarpa, Consolida regalis, Erodium cicutarium, Fumaria officinalis*, *Sinapis arvensis*) and two germinated best in darkness (RLG ≤0.40; *Galeopsis speciosa, Vicia hirsuta*). All of these except *Camelina microcarpa* had relatively large seed masses (Table 1). This, together with the fact that they belong to seven different plant families, showed that light consistently seems to be less important in large-seeded species.

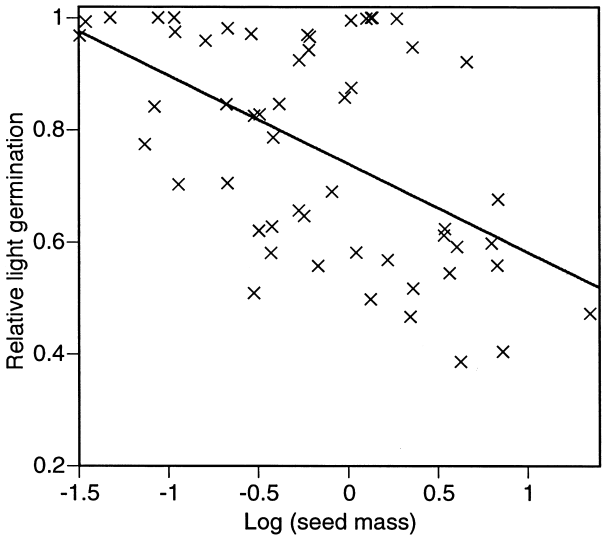


Figure 1. Relationship between seed mass and relative light germination. Y = −0.1577X + 0.7402; R^2 = 0.2774; P <0.0001.

The seed batches used in our study all come from a temperate part of the world, and the pattern detected might not be universal. In fact, the response to light can be reversed: in a Mediterranean climate, light inhibits germination and especially so in small-seeded species (Bell *et al*., 1995), suggesting a scenario where germination on the surface of a rapidly drying soil might be especially detrimental for the seedlings of small-seeded species. Nevertheless, it is always difficult to compare studies that incubate seeds in different conditions (Baskin and Baskin, 1998). Bell *et al*. (1995) used a relatively high photon fluence (80 μmol m^{-2} s^{-1}) which could possibly explain the discrepancy between their results and ours. It is also possible that the large number of weed species from regularly cultivated arable land included in our study has biased our results towards a more profound association between light response and seed mass.

Since we were interested in evolutionary as well as ecological patterns, we also analysed the relationship between seed mass and RLG after taking phylogeny into account. In this analysis, there was also a significant negative relationship between seed mass contrasts and RLG contrasts (Fig. 2; $F_{(1, 39)}$ = 17.48, P <0.001). Two moderately large negative RLG contrasts appeared near the root of the phylogeny. The first distinguishes grasses from dicots, while the second separates the subclass Asteridae from the remaining dicots. Therefore, it appears that the clear relationship between seed mass and RLG in modern angiosperms is at least partly accounted for by some ancient phylogenetic divergences.

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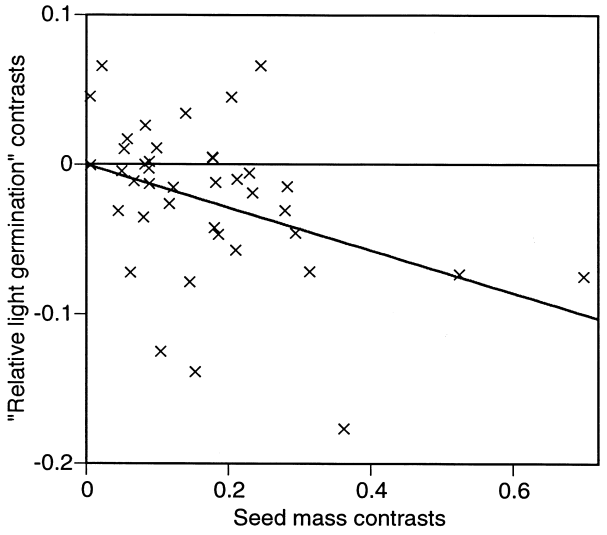


Figure 2. Relationship between seed mass contrasts and relative light germination contrasts (regression forced through the origin). Y = −0.1430X; P <0.001.

Adaptation to a frequently disturbed habitat could partly explain why seed mass and light requirement in some cases are not related. In an environment where disturbances occur with more or less regular intervals, as on arable land, seeds will be subjected to short light exposures in conjunction with soil cultivation or seed bed preparation (Scopel *et al*., 1994; Milberg, 1997). Since such exposures indicate times suitable for seedling growth, it is possible that there might have been a selection for using a short light exposure as a germination cue that detects the optimal time of germination in annual weeds, rather than just nearness to the surface.

Conclusion

We conclude that a light requirement for germination is more likely in small- than in large-seeded species and that its likely ecological role is to sense depth of burial. Furthermore, the relationship remained even after taking phylogeny into account, suggesting that the light requirement coevolved with seed mass.

Acknowledgements

PM and LA were supported by the Swedish Council for Forestry and Agricultural Research and KT by the UK Natural Environment Research Council. We thank referees for valuable comments.

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Received 16 April 1999
accepted after revision 15 November 1999
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https://doi.org/10.1017/S0960258500000118 Published online by Cambridge University Press

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Seed Biology and the Yield of Grain Crops

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The food supply to an expanding world population is based on grain crops, i.e. crops harvested for their seeds. Therefore, understanding the process of seed growth and its regulation is crucial in our efforts to increase production, in order to meet the needs of that population. Yield is determined by the ability of crop plants to use their assimilatory processes such as photosynthesis and also the biosynthetic processes in the seed, which are partly regulated within the seed itself.

This book examines the determination of grain crop yield from a new and unique perspective, by concentrating on the influence of the seed. All aspects of seed growth and development are described, including environmental and genetic effects on growth rate and length of filling period. The effect of the seed on the two main yield components, individual seed weight and number of seeds per unit area, is then discussed. Finally, the concepts and models developed are evaluated in terms of crop management. The book is essential reading for those concerned with seed science and crop yield, including agronomists, crop physiologists, plant breeders, and extension workers. It will also be a valuable source of information for lecturers and graduate students of agronomy and plant physiology.

Contents:

- Introduction
- Seed Growth and Development
- Seed Growth Rate and Seed Fill Duration: Variation and Regulation
- Yield Components – Regulation by the Seed
- The Seed, Crop Management and Yield

May 1998 184 pages HB
ISBN 0 85199 241 2
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https://doi.org/10.1017/S0960258500000118 Published online by Cambridge University Press

Seed Health Testing: Progress Towards the 21st Century

Edited by J D Hutchins and J C Reeves, National Institute of Agricultural Botany, Cambridge, UK

This book is based on selected papers developed from the second International Seed Testing Association (ISTA) – Plant Disease Committee symposium, held in Cambridge in August 1996. Contributors include research workers active in this area from all parts of the world.

The book is divided into five sections. The first discusses new and priority seedborne diseases from the different geographical regions of the world. The second addresses policy issues and is by authors from seed testing organizations, commerce and government. The next section describes new technical developments in seed health testing, particularly the detection of seedborne fungi and viruses using molecular techniques. There is then a group of papers evaluating new methods in comparative tests, conducted by both the ISTA-PDC and the International Seed Health Initiative (ISHI). The final part of the book examines quality assurance in routine seed health testing laboratories and in the production of high quality seed. The book represents an essential reference for all plant pathologists working with seeds and for seed testing laboratories.

Contents:

- SECTION ONE: New and Priority Seedborne Diseases
- SECTION TWO: Developments in Seed Health Testing Policy
- SECTION THREE: Techniques in Seed Health Testing: New Methods and Approaches
- SECTION FOUR: Evaluation of Comparative Tests
- SECTION FIVE: Quality Assurance - Seed Health Testing and Certification

September 1997 288 pages HB
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https://doi.org/10.1017/S0960258500000118 Published online by Cambridge University Press

Essential Oil Crops

E A Weiss, Victoria, Australia

Plants producing an aromatic oil, fruit, or seed have been used in religious ceremonies, for personal use and adornment, and for flavouring throughout history. Today there is still considerable pressure by consumers world-wide to use perceived natural compounds in edible and personal products.

It is essential that producers should be able to service this growing demand efficiently, economically and above all reliably. Additionally, many essential oil crops form part of the economy of countries with growing populations where there is an inevitable pressure on agricultural land as a resource for food and fuel crops. It is therefore important to understand and develop ways of ensuring maximum return on the investments made in establishing and growing these crops.

This book addresses these issues. It is concerned with growing essential oil plants to obtain an aromatic derivative in an economic and reliable manner. Each chapter covers a different family. A brief history of the recent use and economic development of the crop is given and the cultivation and care of the crop is discussed. Current research findings and recommendations for improved agronomic practices are also included. Ways of adding value to the crop, such as extracting the oil, are also discussed.

This book is the key reference work for all researchers and agronomists concerned with essential oil crops. Agricultural advisors and development workers will find the book an invaluable resource and it also contains much information of relevance to commodity traders and policy makers working in this area.

Contents:

- World Trade in Essential Oils
- Annonaceae
- Geraniaceae
- Gramineae
- Lamiaceae
- Lauraceae
- Myristicaceae
- Myrtaceae
- Oleaceae
- Piperaceae
- Rosaceae
- Rutaceae
- Santalaceae
- Zingiberaceae
- Distilling and Extracting Essential Oils

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Azuki Bean: Botany, Production and Uses

T A Lumpkin and D C McClary, Department of Crop and Soil Sciences, Washington State University, USA

Azuki is one of the twelve most important grain legumes in the world and is grown widely in China, Japan, South Korea and Taiwan. It has also been produced or studied in several other countries, including the USA (Minnesota and Washington States), Argentina and Australia. In Japan, azuki is an essential ingredient of both *seki-han*, a festive rice dish, and *an*, a sweetened bean paste. Botanically, it formerly belonged to the genus *Phaseolus*, but it has recently been transferred to the genus *Vigna* with relatives such as mungbean, black gram and rice bean. This book is the first comprehensive work on this crop. It draws extensively on the Chinese, Japanese and other East Asian literature and is based on a review of approximately 800 published references. It is a definitive reference work that should greatly enhance interest in the crop. It is aimed at researchers throughout the world working on grain legumes, as well as others in agronomy and plant science.

Contents:

- Foreword *Kazumi Maeda (Kochi University, Japan)*
- Introduction
- Botany of azuki
- Physiological characteristics
- Production
- Insects and nematodes
- Diseases
- Breeding and genetics
- Food chemistry and processing
- Uses and marketing

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