THE PRINCIPLES OF POLLINATION ECOLOGY

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THIRD REVISED EDITION

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PREFACE TO THE THIRD EDITION

The object of this book is stated in the title: *principles* of pollination ecology. It is not a manual. A comprehensive manual of pollination ecology would run into many volumes; indeed, Knuth's handbook dating back to the turn of the century covers 2972 pages, and very much has been added to our knowledge since then. Besides, such a manual would chiefly contain redundant or irrelevant matter, dealing with plants of little or no direct interest except for the few scientists specializing in pollination ecology. What might be desirable is a set of regional manuals, geared to the local floras or treating families or other major taxa in a systematic fashion. One or two such manuals might be written today, and might also count on reader interest, sufficiently widespread to warrant publication. However, that is not the task we have set ourselves, and when we quote specific examples it is simply to give concrete demonstrations of how pollination functions in practice. We make no attempt at being complete: for each example quoted, probably dozens of others might just as well have been used. We may also neglect aberrant types: we quote the genus *Cornus* as an example of plants in which the bracts are enlarged and form visual attractants – notwithstanding the fact that in *C. mas* the flowers are equally important in that respect. For examples that belong to general botanical knowledge, we do not, as a rule, quote any authority; such quotations would have inflated the size of the book, and most of them can be found with details in Knuth's handbook (of which the original third volume was unfortunately never translated, vol. 3 of the translation being vol. II, 2 of the original.) Personal observations are sometimes initialled, especially if unpublished.

We have tried to formulate *general principles* of pollination ecology, applicable anywhere, and it is our hope that the reader will acquire a sufficient measure of these general principles to make his own observations within the confines of the flora of the area in which he is living.

We cannot here describe all the different ways in which, for example, stamens are modified in response to pollination: what we can do, and what we hope to achieve, is to make the reader aware of the problem of, and the existence of, variations in the androecium and the possibility that these variations may, in one way or another, be functionally explicable in terms of the pollination ecology of the flower in question.

Thus, it is our hope that the book will help first the college or university teacher, giving him the necessary background for teaching pollination ecology to his students, and secondly, those students when they go back to schools (as many of them will) and in their turn take up teaching, whether this happens in an area with a similar or a different flora. Further, it is hoped that the book will serve the college or university student as a frame of reference to which the concrete data of the courses can be referred, and where he can find the general principles behind the individual observations he is able to make in the field or laboratory.

This book should therefore not be studied in isolation. Metaphorically speaking, one should hold it in one hand, the living plant in the other, correlating the concrete facts of the latter with the general principles of the former. The aim of the book is to give the reader the potential for a more profound understanding of what he may have seen many times, but has never observed. Perhaps it is not superfluous to stress the importance of observations of what actually happens in nature. Too many erroneous conclusions about pollination ecology have in the past been made from morphological observations, in gardens, or by laboratory experiments alone. The only phenomenon that is really valid is what happens where the plant is growing spontaneously. Ecology deals with the interaction between organisms and their habitats, and while it is very interesting to observe pollination in plants that have been transplanted outside their proper area, this only gives information about the adaptability of pollination agents, not about the mutual adaptation of flower and agent (see van der Pijl 1937a).

"Modern" biology has made spectacular advances during the last few decennia. The results of genetical, biochemical, and other investigations have given us a new insight into phenomena of life never before understood, hardly even perceived, but to a majority of biologists many of the spectacular achievements of modern biological research can be but a theoretical knowledge, to be learnt from textbooks, theses, or in the lecture hall. Many phases of "old-fashioned" biology can be studied, albeit primitively, by and brought home to every schoolchild. To deprive him or her of the opportunity of this direct contact with nature is, we think, wilfully to take away the bread and offer stones instead, be these stones full of precious minerals. Pollination ecology is therefore a subject of the greatest value in teaching, just because the teacher who knows the basic principles can make them come alive everywhere, to all his students (Webb 1957).

The three R's may seem trivial, but they are fundamental. Too many "modern" biologists seem to forget the importance, not only of those three R's, but of a long series of other ones, leading up to the summits of today's science. "Nature study" (including pollination ecology) may perhaps seem rather far down the ladder, but it is our conviction, unfortunately confirmed by *bêtises* on the part of "modern" biologists, that a biology neglecting these apparently simple branches is doomed to sterility, and that the functional aspect is all too frequently neglected.

This does not, of course, mean that pollination ecology should not benefit by the achievements of modern biological research. Not entirely without reason pollination ecologists have in the past been accused of neglecting the results of research in other branches of biology. However, this situation has changed materially in recent years, and it changes from day to day, not only in the use of sophisticated equipment, but also in the integration with ideas from evolution, ethology, etc.

To illustrate the principles of pollination ecology we have described some case histories as examples. For practical reasons the nomenclature of the original publication is usually retained when cases have been quoted from the literature.

Using this book in the field a reader may feel that too many of the examples have been taken from too few floristic regions. The explanation is simple enough: pollination ecology has chiefly been studied in a few areas, and so we have had to take our examples from them. We have a small, but fervent, hope that this book may initiate studies in pollination ecology in other regions. Should this be achieved we are in no doubt that not only would it be possible in future books on this subject to supplement our examples by better ones from other floras, but also that completely new principles may come to light, corresponding to the discovery of the sexual attraction, or the pollinating marsupial. If this book rapidly becomes outdated for that reason, nobody would be happier about it than the authors.

So far we have mainly quoted from the preface to the first edition. Since its publication, the position of pollination ecology has changed from being a backwater of biology to become an important field of research, as witnessed by the multitude of research papers – far too many to be adequately covered – and several textbooks aimed at various levels. The increased activity, for which this book may be partly responsible, has many causes; one of them is the practical importance of understanding the pollination ecology of crop plants for high yield and for purity of strains. Also, modern research in pollination has revealed many important facets of biological evolution. What some twenty years ago seemed a rather static subject, fixed in its conceptual foundation, is today in the process of reorienting itself towards a higher level of understanding of basic principles. Also taxonomists are increasingly aware of the importance of pollination ecology for speciation, a subject completely neglected earlier, and modern taxonomic monographs tend to include pollination data.

We have chosen the term pollination ecology for precision. We understand "floral biology" to comprise all manifestations of the life of the floral region, also those not directly connected with pollen transfer, even if they interact with the phenomena that are treated in this book. Our aim has been to discuss only the interaction of plants and their pollination vectors, the ecological problem.

L. van der Pijl
K. Fægri

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CHAPTER 1

A SHORT HISTORY OF THE STUDY OF POLLINATION ECOLOGY

1.1. THE SEXUALITY OF PLANTS

Certain agricultural practices with the aim of achieving or furthering the production of fruits or seeds by cross-pollination have been known, perhaps, as long as organized agriculture has existed (see Chapter 16). Some of these practices are recorded in documents from classical and pre-classical ages; we may assume that there have been others.* Even so, the scientific concept of what pollination represents took a remarkably long time to establish itself, and the idea of sexuality in plants, whether it existed and how it manifested itself, was a standard problem during the Classical Age, the Scholastic Period, and even during the first centuries of more modern science. The question was frequently settled by criteria for maleness and femaleness which we cannot now accept as valid, for example those expressing themselves in still existing names like *Athyrium filix-femina* and *Dryopteris filix-mas*. As can be surmised, the scholastic argument in this case makes a rather amusing lecture, but does not contribute much to a solution of relevant problems. Perhaps it is more than a coincidence that the sexually repressed Middle Ages could not grasp an idea which presented no difficulty to the more licentious eighteenth century (see Taylor 1954).

It was left to the age of Linnaeus to solve the problem. He himself realized the importance of the so-called sexual organs of the flower, and based his division of the plant kingdom on them. However, his own contributions to pollination ecology are insignificant, and there were other botanists of that era to whom we are more indebted.

To Rudolf Jakob Camerarius (1665–1721) we owe the recognition of the sexuality of plants and the understanding of the function of the sexual parts of the flower. In a published letter *de sexu plantarum* (1694), based upon his own experiments, he states that two different parts of the flower, viz. stamen and pistil, must work together to produce ripe seed. He concluded, therefore, that these two parts represented the sexual organs, a concept still generally maintained, even though it is not quite to the point. The flowering plant represents the asexual diploid generation, therefore it is not strictly accurate to call its organs sexual.

1.2. CROSS-POLLINATION. THE FOUNDATION OF POLLINATION ECOLOGY

Self-pollination of the bisexual flower was apparently so obvious to Camerarius that he never thought about other alternatives, and the first discoveries of cross-pollination are said to be due to A. Dobbs (1750) and H. Müller (1751) who also discovered the rôle played by insects in pollination (Sachs 1875, V. Grant 1949a). However, neither Dobbs nor Müller

*For the history of pollination ecology with references, see Loew 1895; Lorch 1966; Schmid 1975.

pursued their studies, and two other botanists, Koelreuter and Sprengel, are generally accepted as the fathers of pollination ecology.

Joseph Gottlieb Koelreuter (1733–1806) was the first botanist to carry out hybridization on a large scale for scientific purposes, thereby definitely proving the sexual nature of pistil and anther; he described the pollen grain and its function in some (not always correct) detail, and defined the stigmatic surface as a separate part of the surface of the pistil. He recognized autogamous, anemophilous, and entomophilous pollination, and the rôle of the nectar. He also recognized dichogamy and the function of certain movements of floral parts. Koelreuter's main work on pollination was published 1761–6.

The next major publication was Christian Konrad Sprengel's (1750–1816) famous work published in 1793. Without knowing about Koelreuter's paper he rediscovered entomophily and dichogamy and interpreted their importance more correctly. In the same way, he found that cross-pollination was obligatory in some plants. Among his other discoveries, based upon innumerable individual observations, were nectar protection, nectar guides, trap flowers, the function of the corolla as an organ of advertisement, and the differences between day and night flowers. His main discovery was that of the mutual adaptation of flowers and their pollinators. Pollination ecology before and after the publication of his book were two different things.

1.3. THE PRE-DARWINIAN PERIOD

The period between Sprengel and Darwin is one of almost complete neglect of pollination ecology, and prevailing concepts were generally much less advanced even than those of Koelreuter. However, the studies of pollination ecology of Darwin and his contemporaries presumed the understanding of floral morphology and of the fertilization process gained during this period.

For pollination ecology itself only one name may be mentioned from this period: Thomas Andrew Knight, who in 1799 formulated the principle that no plant can without detrimental effects pollinate itself for a sequence of generations. This principle was based upon observations of the behaviour of obligate outbreeders and was later, under the heading of the Darwin–Knight law, to play a rather unfortunate part in pollination ecology, leading less critically minded followers of Darwin to neglect the phenomenon of self-fertilization, and to search, sometimes rather frantically, for cross-pollination mechanisms and adaptations even in habitual inbreeders.

1.4. DARWIN AND THE POST-DARWINIAN PERIOD

Charles Darwin influenced pollination ecology more deeply than anybody else during the nineteenth century. Within this field he published a number of papers that gave evidence of patience and acuity of observation. Pollination ecology had not made such progress since Sprengel's time. His methods of observation marked the end of the deductive, philosophical approach of the previous half of the century.

Even so, Darwin's most important contribution to pollination ecology was of a more profound nature. To Sprengel the wonderful adaptations he observed in his flowers were witnesses of the Creator's wisdom and of the beauty of His creation. This admirable view point could hardly appeal to scientists at large, and pollination ecology would therefore tend to assume the character of a mass of uncorrelated facts. The acceptance of the theory of natural selection immediately changed this situation: adaptation, not to speak of mutual adaptation, was one of the phenomena, indeed *the phenomenon*, at the centre of interest of early selectionists; the study of pollination ecology with its remarkable adaptations became scientifically fashionable, and, more important, acquired a new philosophical dimension, and a unifying theory.

Whereas it is almost impossible to find a single botanist worth mentioning in pollination ecology during the first half of the nineteenth century, their names abound later to such an extent as to make any attempt at a complete enumeration futile. The two Müllers, Hermann and Fritz, Federico Delpino (to whom we owe many modern terms and concepts), Friedrich Hildebrand, and many others (e.g. Trelease and Robertson in the U.S.A.) were busily collecting data on pollination, sometimes with more eager than critical judgement. This period culminated in Knuth's great work from 1898 to 1905, which was completed by Loew. It contains all data known up to then and is still a most useful work of reference, though usually no more critical than the individual papers on which it is based.

1.5. THE MODERN PERIOD

Classical pollination ecology had apparently spent itself with Knuth's handbook. Its philosophical approach and methods were obsolescent, and the study of pollination more or less fell into disrepute during the first decennia of our century as an occupation for retired schoolteachers, but unworthy of a real scientist, even if noteworthy contributions were published during this period, e.g. by Clements and Long. The impact restoring it came from outside, from the study of animal behaviour. The studies of Frisch, Knoll, Kugler, and others on the behaviour of different groups of pollinating insects had important repercussions on pollination ecology because the results of these studies gradually restored confidence in many of Sprengel's acute observations and deductions which had been discredited by a previous generation.

Modern trends in pollination ecology can be summarized under the following headings: (1) Observations in countries outside Europe. Most of the work done by previous generations had been carried out in Europe, even exotics being studied in European botanic gardens. As important classes of pollinators are absent from the European fauna this led to grave errors. (2) The experimental approach to verify deductions and to test the reactions of pollinators. (3) A genetic and phylogenetic (also population genetic) approach to the problems underlying phenomena of pollination ecology, and a more profound genetical understanding of the implications and importance of cross-pollination. (4) As a consequence of this, pollination data ("breeding system data") are now gradually being incorporated into biosystematic reasoning. (5) Quantitative data about the energy flow in plant/pollinator interaction. (6) The realization that pollination ecology must be seen in a total community context, even if there are few quantitative data in literature as yet. Until now, the evolution of community pollination spectra has only been touched upon.

CHAPTER 2

TECHNIQUES IN POLLINATION ECOLOGY

The primary technique of pollination ecology (cf. Porsch 1922) is the same today as in Sprengel's or Darwin's days: consistent observation of what really happens in nature, in the original, natural habitat of the plant under investigation. A plant growing in strange surroundings is exposed to other pollinators which may work the pollination mechanism "correctly" or may not. Even wind conditions may differ in a foreign habitat. An "incorrect" pollination mechanism may be of great interest in itself, but, as previously mentioned, it will not give information about the existence of mutual adaptations between that particular plant and the fauna of the region. The fact that, for example, American ornithophilous flowers in the Old World are pollinated by local birds belonging to taxonomic units completely different from the American ones, proves the general character of ornithophily, but gives no information about the specific adaptation mechanisms.

Straightforward observations as to how pollination is carried out are not always made without difficulty. Some pollinators work at inconvenient times of the day, or out of the reach of ordinary visual observation, e.g. in tree-tops. In other cases it may be desirable to watch the behaviour of individual pollinators, which necessitates marking and other complicated techniques. Or pollinators may have to be captured and investigated for their nectar and pollen loads, both on the outside and in the alimentary canal. All classes of visitors should be recorded. One sometimes suspects that some of the classical investigators have discarded observations or overlooked insects because of a preconceived notion that they did not "belong", or because they were too small, etc. That both plants and animals should be properly identified and voucher specimens kept is another obvious admonition. Periodicity in the appearance of attractants and of suspected pollinators is an important fact that should be closely observed.

The movements of pollinators in flowers are frequently very swift, and often photographic techniques are desirable to analyse the behaviour of animals, sometimes also the function of floral parts. Modern photographic techniques – powerful flashlights, stroboscopic light systems, rapid colour film, on-the-spot developing – have immensely increased the potentialities of photographic methods. Photomultiplying devices are important in the study of pollination. Ayensu (1974) gives very good night photographs of pollinators and fruit-eating bats taken without additional light. Cinematographic techniques are even more valuable than still-photography. Pollination observations in the field are always extremely time-consuming, and days may pass without anything happening. Photographic techniques may take even longer, because it usually does not pay to run after the pollinator with a camera; it is better to focus one or a few blossoms and wait until the pollinator arrives.

In some respects television techniques are superior to photographic techniques and visual observation: the potential wavelength spectrum is wider and results can be obtained with lower light intensities. Combined with video techniques they give an instantaneous permanent record (Eisner *et al.* 1969).

The wing-beat of insects, especially bumblebees, changes with different activities. Tape recordings have been used to analyse this. Some of Macior's recent papers give examples of very refined field techniques.

In the field there are also negative observations to be made. Sometimes it is as important to note which animals do *not* visit, though present in the locality. And, similarly, it is important to note which animals visit other blossoms in the neighbourhood instead of, or together with, the species under observation.

Hagerup (1951) has rightly pointed out that insect visits, even regular insect visits, to a flower do not always mean that the particular insect is the pollinator of that flower: there is always a chance that autogamy may have occurred earlier, even before the flower opened, or that some other less conspicuous insect may have carried out the pollination. The state of the stigma should therefore also be checked before the pollination act under observation.

Very simple equipment may help to supplement the field observations. Odour-producing organs within the flowers (osmophores) can be localized by cutting out the suspected parts and keeping them for some time in a closed vial. The accumulated odoriferous gases are easily smelled when the vial is opened. The presence or absence of sticky or oily substances on pollen grains or on animals can be checked by bringing the organ in question into contact with a clean glass plate on which traces of oil are easily seen (Daumann 1966). Self-pollination is checked by enclosing flowers in a bag sufficiently tight not to let insects (or wind-dispersed pollen) in, taking care that temperature and humidity inside the bag do not rise to dangerous levels.

Chemical analyses of varying degrees of sophistication are necessary for the identification of nectar constituents or active liquid or gaseous substances in or emanating from the flowers. Thin-layer and gas chromatography are obvious methods for the solution of many of these problems.

Physical techniques used are spectral analysis of flower colour, both inside and outside of the visual spectrum, or electrophysiological techniques, especially for the study of sense reactions, e.g. electroantennograms for the study of odour perception, Kullenberg and Stenhagen (1973) give many examples of the use of refined chemical and sense-physiological techniques in the study of pollination, above all various phenomena of sexual attraction.

Pollen adhering to pollinating insects indicates which species have been visited. The pertinent palynological techniques are presented elsewhere (Fægri and Iversen 1975).

The next question is why pollinators behave as they do. Conclusions by analogy may be of considerable help, but in many cases experiments are necessary to decide between hypotheses. It is not easy to carry out conclusive experiments on ecological questions, and all too frequently "no effect registered" has been interpreted as "no interrelationship extant", which is not always the case. Some of the more common errors are abnormal behaviour of many insects when caged, different colour perception, due to the effect of radiation invisible to the human eye and different behaviour of conditioned and "virgin" pollinators (a nectar guide may greatly help an inexperienced pollinator, but be of no value or have a different meaning to one that has previously visited many flowers of the kind, cf. Kugler's different evaluation of the function of nectar guides in 1930 and in 1936). In reality the "why" of pollination ecology is largely animal psychology, and experiments in pollination ecology without a thorough background in animal psychology are generally less valuable than simple field observations as to "how".

Earlier observers presumed that the senses of pollinators, which then meant pollinating insects, corresponded to those of man. Today we know that they do not necessarily do so, but in modern experiments it is often astonishing to see how similar are the effects of sensory activity in insects and in man (see Ribbands 1955). However, there are also obvious exceptions, like different ranges of the visual spectrum (Kugler 1962), the presence of chemical contact receptors on extremities, or special smells connected with sexual activity (see Kullenberg 1956b and later). One rather specific, but very serious source of errors in experiments of this kind is that both the experimenter and his animals ultimately become too clever, and the latter may be trained to perform tricks never performed under natural conditions.

However important, and often indispensable, physiological or morphological analyses are for understanding ecological adaptation, they cannot replace the ecological, functional aspect, any more than the chemical fact that the blue paint is ultramarine explains why the artist has decided to use blue at that place in the painting.

Pollination processes are particularly well adapted for cinematographic representation. For example, the films issued by the Institut für den wissenschaftlichen Film, with comments by Vogel, or the Uppsala *Ophrys* films (Kullenberg and Bergström 1976) are of very high scientific and educational quality.

CHAPTER 3

POLLINATION AS SPORE DISPERSAL

Although pollination exists only in higher plants, i.e. those possessing pollen, it is, in fact, a specialized type of a phenomenon that occurs throughout a major part of the vegetable kingdom. To forget this tends to confuse the issues and to present pollination as something more complicated than it really is. For a proper understanding, pollination must be referred back to related phenomena in lower plants. As we see it in nature, the phanerogamic plant represents the diploid generation, the sporophyte. As the name implies, this generation produces spores, generally accompanied by chromosome reduction. These spores germinate into the haploid generation, the gametophytes, which are male or female, and produce sexual cells that fuse again at fertilization, thus reconstituting the diploid number and producing a new sporophytic generation.

Schematically, this can be represented, e.g. in the green alga *Ulva*, as follows:

sporophyte → reduction division → spore →
gametophyte → gametes → fertilization → sporophyte

In *Ulva*, all specimens have the same sexual potentiality; in others, e.g. *Selaginella*, there are two types of spores, producing two different types of gametophytes:

sporophyte → reduction division ↗ microspores → / ↘ macrospores →

male gametophyte → spermatozoid ↘ / female gametophyte → egg cell ↗ fertilization → sporophyte

A corollary to the existence of two types of spores is the need for two different dispersal strategies. Pollination is related to microspore dispersal strategy only.

Phanerogams also produce macro- and microspores, but the macrospore is included in the pistil, and never becomes a discrete unit. As its presence is therefore generally not realized, this makes the microspore, i.e. the pollen grain, appear more exceptional than it really is, because of the apparent absence of a female counterpart. Actually, apart from the existence of a few gametophytic cells (mostly abortive), there is little to distinguish between a young pollen grain and a typical microspore. In a wider biological sense, pollination is simply a specialized case of microspore dispersal, and pollination ecology a special aspect of spore dispersal ecology. The nuclear divisions taking place in the pollen grain later do not influence its dispersal strategy and can therefore be neglected in this comparison.

Apart from the most primitive ones, plants have two sedentary stages, sporophyte and gametophyte, and two mobile or motile ones, spores and gametes. Originally there was not much difference between (zoo-)spores and gametes, but gradually spores changed as a response to ecological conditions. During phylogenetic development gametes did not change very much, except that ultimately they were so reduced as almost to lose their individuality. The uniformity of gametes entails that the fertilization process is also rather uniform throughout the plant kingdom. Even in angiosperms the main features of fertilization are not very different from those of the more primitive process in lower plants.

With gametes being confined to the original aquatic (or at any rate moist) conditions of primitive plants, spores are the stage adaptable to dispersal under dry conditions, and the existence of terrestrial plant life presupposes the existence of spores resistant to the adverse forces of land life. We see, therefore, that spores even of the most primitive land plants have a resistant outer cover that is chemically related to that of pollen grains. For their pollination higher plants were thus able to take over an already existing spore type and a mechanism already developed for its dispersal.

Yet in one respect there is a very great difference between spore dispersal and pollination. An ordinary spore has a comparatively wide ecological niche; even if a gametophyte may be rather exacting in its demands (not all of them are), there are many places and many types of habitats in which the spore may germinate. Further, being motile, the gamete(s) can to some extent compensate for an unfortunate mutual position of the male and female apparatus. The pollen grain, on the other hand, can germinate and the gametophyte grow successfully in one single, very restricted place only, viz. on the stigmatic surface of a compatible flower. If germination exceptionally takes place elsewhere, the resultant plant, the pollen tube, cannot fulfil its biological function, or even develop properly.

This enormously restricts the germination potential of pollen grains and calls for a much greater *precision in the transfer* than in the dispersal of ordinary spores. The many remarkable adaptations (Section 5.1) observed in pollination ecology can only be understood against the background of this demand for precision, and the evolution of pollination mechanisms in entomophilous blossoms is, on the whole, an evolution towards increasingly higher precision.

With the evolution of heterospory in many lower plants, a certain demand for precision in the transfer of the microspore will establish itself in these groups as well, modified by greater or lesser motility of the "male" cells themselves.

In higher plants, one of the primary ecological functions of the spore in lower plants, viz. dissemination, has been taken over by an entirely new dispersal unit, the seed, an arrested developmental stage of the new sporophyte. Ecologically the seed may be compared to the resting zygote of lower plants. Seeds have a much wider ecological range than pollen, to which corresponds the fact that seed dispersal mechanisms are generally less evolved (but not always less varied) and function less precisely than pollination mechanisms.

For a proper understanding and evaluation of pollination mechanisms, we shall first recapitulate the main features of spore dispersal in lower plants.