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Variation in Anthesis and Pollen Production in Plants

V.P. Khanduri

Department of Forestry, Mizoram University, Aizawl (Mizoram)

Abstract: Flowering is of prime importance in plant's life and in breeding, which determines generation turn over and genetic gain. It has been established that the flowering is under genetic control but highly influenced by the environmental factors. The quantum of flowering and pollen production is inconsistent, abundant in some years and meagre or absent in others at individual and community level, affect the degree of genetic variability in each species. In the present review, information were brought together and evaluated on this subject particularly the regulation of anthesis by temperature, relative humidity and light alongwith the consideration of the role of pollen production in pollination and fertilization.

Key words: Anther dehiscence · Pollen grains · Pollination · Pollen output

INTRODUCTION

The transition from the vegetative to the reproductive stage is one of the important morphogenetic events in the lifespan of a flowering plant. It involves manifold changes in the metabolism and arouses several formative processes connected with the onset of sexual reproduction and alternation of generation [1]. The study of the behaviour of male gamete (pollen grains) is an essential pre-requisite for acquiring knowledge about the inheritance patterns and for subsequent improvement and breeding programmes. Pollen grains are containers which house the male gametophytic generation and require dispersal in space and time. Pollen grain can only be regarded as having served its purpose successfully if it arrives at the stigma (or micropyle) of a plant of the same species and germinates there with subsequent fertilization of an egg.

Knowledge of anthesis and pollen production is essential to the study of pollination, developing a functional model for forecasting pollen concentrations and to understand more about the ecological background of pollen dispersal. Yet attempts for gaining such knowledge are few and the methods employed are not uniform [2, 3]

The flowering processes of grasses have been studied for over 100 years [4] and it soon became customary to describe the flowering habits of species in relation to fertilization [5-10]. In 1931 Jenkin [11] studied flowering habits and developed new methods and techniques in grass breeding. Also in 1931, Beddows [12] gave a survey of literature up to this date, with descriptions of flowering habits in 64 grass species.

In the current scenario of global warming, flowering time is considered as the best way for judging the climatic change at local and global scale [13]. The flowering time of each species is genetically fixed, which is highly variable with the environmental factors, mainly precipitation and temperature. Climate change has affected many aspects of the biology of trees and its effect on plant's first flowering dates would be of great significance [14-15]. Therefore, reproductive phenological analysis of trees in terms of anthesis and anther dehiscence provides a potential tool to unravel critical questions related to monitoring and modelling of climate change. In recent years, the focus of such studies has shifted to questions of how reproductive phenology will be affected by climatic factors and what consequences any climatic change may have for species distribution and ecosystem function. Plant communities show conspicuous seasonal pattern in vegetative and reproductive phenologies at both community and species levels particularly to tropical plant [16-17], which with the interaction of climate change extended the growing season by 1.8 days year^{-1} [18].

Anthesis: The anthesis is an active process based on the physiological and ecological behaviour of a plant. The anthesis and pollen release are important criteria for assessing the subsequent dispersal of pollen grains into the ambient air. Dehisced or split-open anthers give us accurate estimates of the daily pollen release, which is a

Corresponding Author: V.P. Khanduri, Department of Forestry, Mizoram University, Aizawl (Mizoram).

prerequisite for knowing the pollination system and breeding behaviour of species particularly anemophilous taxa at a given place.

Anthers are found both in uni-and bisexual flowers that range in shape from spherical to prismatic, with various size at elongation. The development of pollen occurs in a cavity known as the loculus where the Locular fluid carries nutrients from the sporophyte to the developing male gametophyte. Anthers mostly contain four locules but the number varied from two or more. At different stage of anther development, the composition of locular fluid changes and the concentrations of dissolved substances decline sharply with the maturity of pollen grains. The anthers are hold by filaments which in the mature flower occurs erect, curved or pendant depending on the mode of pollination. The filaments are responsible for the presentation of pollen on the dehisced anther to the pollinators and their release. The presentation of pollen to dispersing agents is possible only after anther dehiscence (an important phenomenon highly dependent on the climatic factors). Anther dehiscence is preceded by losing of the locular fluid. The water content in the pollen grains varied from 5 to 50%, depending on the species. Transfer of pollen may occur in monads or grouped in pollen dispersing units as: (i) filamentous pollen tangling; (ii) pollen stickiness by viscous substances (pollenkitt, tryphine, elastoviscin) exuded from the tapetum; (iii) common walls. Anther dehiscence follows primary presentation (immediate dispersion of pollen) or secondary presentation (available to pollinators in other flower parts).

The work on anthesis was first done by De Cugnac and Obaton [19]. In 1941 Davidson [20] stated in an article on anthesis and the relation of anthesis to collection of pollen for medical purposes: "Each species shed its pollen at its own time of day and often with clock-like regularity". Who also suggested the use of a method to collect pollen in relation to anthesis. The effect of climatic factors viz., air temperature, relative air humidity, light intensity and wind on five grass species (*Alopecurus*, *Dactylis*, *Festuca*, *Lolium* and *Phleum*) have been carried out by Emecz [21], who found that anthesis was positively related to temperature and light by which it was activated. Relative air humidity did not have any significant direct effect, but it casually inhibited anthesis through reducing light intensity or through precipitation. Environmental effect may exceed varietal differences which were significantly genetical in origin. Who also suggested that grasses can be grouped according to the velocity of their physiological responses to environmental effects and that the groups may be called 'quick-staminating' and 'slow-staminating'. Liem and Groot [22] have recorded that the climatic factors were related to anthesis and pollen dispersal in *Holcus* and *Festuca.* They found that in both the species the anthesis showed a diurnal periodicity which were connected to air temperature, relative air humidity and light intensity. However, Liem [23] worked on the effect of light (light intensity and light period) and temperature on anthesis processes of *Holcus lanatus*, *Festuca rubra* and *Poa annua* under experimental conditions in a climatic room and concluded that each of the studied grass species possesses anthesis patterns based on specific characters which are not influenced by light intensity or light period. Thus, the unsuitable climatic conditions in terms of low temperature and high humidity may prolonged the anther dehiscence and certainly delaying the pollination which may cause significant reduction in fruit set, fruit retention, fruit weight and chemical characteristics [24]. The temperature regimes also influence both *In-vitro* and *In-vivo* pollen germination and the optimum range vary from species to species [25].

In the vast and scattered literature on anthesis in the agricultural grass species, the work done on anthesis and anther dehiscence in tree and plant species is meagre. Subba Reddi and Reddi [26] reported the anthesis and anther dehiscence on two tropical tree species of Euphorbiaceae (*Cicca acida* and *Emblica officinalis*) in relation to prevailing weather conditions. Bhattacharya and Datta [27] presented data on anthesis and pollen release in some 35 dominant plant taxa of tropical West Bengal. Bimodal pattern of anthesis was recorded in *Grevillea robusta* by Khanduri *et. al.* [28]. According to Sharma *et. al.* [29] and Khanduri and Sharma [30], air temperature and relative humidity sharply influence the anthesis and anther dehiscence in *Pinus roxburghii*, however, light intensity did not have any effect, but the species shows diurnal pattern of anthesis. Roychowdhury *et al*. [31] also observed diurnal pattern of anther dehiscence in *Morus* sp (Mulberry) with peak period of anther dehiscence (PPA) during 10.00-11.30 am and 3.00-4.00 pm.

Pollen Production: The estimation of total pollen production per plant is useful not only from an aerobiological but also from an agronomical stand point, as the production of seeds often depends on the production of pollen [32-35], moreover the efficiency of anemophilous pollination decreases with the reduction in the concentration of air borne pollen [36]. Holm [37],

demonstrated that by adding a supplementary amount of pollen to *Betula* an increase in the quantity of seed produced can be obtained. A plant's total production of pollen grains is influenced by various factors [38] and also varies from lower altitude to upper altitude and from one year to the next [39-41]. The initial conditions generally favouring pollen grains production are warmth, dryness and sunshine during formation of flower primordia on the previous year, favourable precipitation during the vegetative growing season, lack of winter killing and sunshine prior to pollination. The environmental factors influencing the pollen production of a variety of deciduous trees and spruce and pine were reported by Scamony [42].

One of the first and most complete studies on the amounts of pollen produced by a plant was that carried out by Pohl [43-44]. In both the studies, information was provided about the quantity of pollen produced per anther, flower, inflorescence and branch in some herbaceous and anemophilous tree species. The values of pollen production per plant in several herbaceous species [43], varied between almost three million to a little more than 1300 million (the maximum value pertaining to *Mercurialis annua*). However, woody plants viz. *Pinus sylvestris* produce 152×10^3 to 162×10^3 pollen grains per flower [44]. Data was also provided about the quantity of pollen per square meter of land surface produced by some plants by calculating the projection of the plant on the soil and the number of flowers per individual. In 1943 Erdtman [45] added data to complete Pohl's study [35, 36] and in 1969, Erdtman [46] presented a Table of 19 species for which he calculated the number of grains per anther, flower and ament and established an index of relative pollen production, using the value of one as a reference for *Fagus sylvatica*. Who affirmed that there is a clear tendency towards an increase in the production of pollen grains in anemophilous plants. Hyde and William [47] made complementary contribution with an estimate of the pollen production per surface unit in *Plantago lanceolata*, calculating the number of inflorescences per square meter of land square, the number of open flowers per inflorescence and the mean number of pollen grains per flower, giving a mean value of $40x10^6$ pollen grains per square meter. Nair and Rastogi [48] made further contribution by studying the pollen production of several species linked to allergy in humans such as *Chenopodium album* (133 pollen grains/anther) and *Morus alba* (23,388 pollen grains/anther).

Joppa *et al*. [49] determined the total production of grains of airborne pollen for different types of *Triticum* from the number of fertile flowers and the percentage of extruded anthers. Rangaswamy and Raman [50] established that in *Oryza sativa* polyploidy caused the number of pollen grains and the size of the anthers to increase, while the ratio between the two decreased. The production of pollen of the family Poaceae was studied by several workers. Agnihotri and Singh [51] recorded 800 pollen grains in *Cynodon dactylon* and 13,000 in *Secale cereale* per anther and suggested that total production of pollen depends directly on the size and length of the anther, calculating a value of 700-1200 pollen grains per millimeter of anther length. They concluded that the pollen production, besides varying greatly from one species to another even within the same genus, was directly related to the size of anther and inversely related to the size of the pollen grains and that, therefore, those species with large anthers and small pollen grains were the most productive ones. Smart *et al*. [52] made an estimate of the pollen production per anther and spike in 30 grass species. By counting the number of spikes per square meter they arrived at an estimate of total production of pollen per surface unit in the between spikes of Gramineae. Thus for *Lolium perenne* they gave a value of $2.11x10^{13}$ grains/season and hectare. Bai and Subba Reddi [53] and Subba Reddi and Reddi [54] determined the pollen production per anther for several Angiospermous species and contended that the levels of pollen production in a particular species is a function of its genotype and the amount of pollen grains per anther might be genetically fixed [49]. The level of pollen production per tree in some Angiospermous tree species was recorded between 15.2-250.1 x 10^9 for *Acer negundo,* 11.2-160.7 x 10^9 for *Fraxinus angustifolia,* 1.8-2.8 x 10^9 for *Lannea coramandelica,* 29.1-108.3 x 10^9 for *Olea europaea,* 114.9-250.6 x 10^9 for *Plantanus hispanica,* 113.0-134.7 x 10^9 for *Populus nigra,* 109.4-633.5 x 10^9 for *Quercus rotundifolia,* 36.0-47.7 x 10^9 for *Salix artocinerea,* 5.0-8.0 x 10^9 for *Ulmus minor* [55]; 0.104-0.116 x 10^9 for *Grevillea robusta* [28]; 2.0-3.3 x 10^{14} for *Shorea robusta* [56]; 24,046-55,045 x 10^6 for *Quercus suber*, 11,919-24,500 x 10^6 for *Q. ilex* ssp. *ballota*, 16,715-22,731 x 10^6 for *Q. faginea* [57]; 9.498-14.208 x 10^8 for *Tectona grandis* [58]. However, in some Gymnospermous tree species the figure reported was 1.9 to 21.6×10^9 for *Cedrus deodara* [41]; 20.9 to 32.3×10^9 for *Pinus pinaster* [55]; 12.5 to 27.3×10^{11} for *Pinus roxburghii* [40] and 1.31×10^9 to 1.74×10^{10} for *Cunninghamia lanceolata* [59]; 64.5×10^9 for *Cupressus sempervirens*, 12.3×10^{10} for *C. arizonica* and 11.4×10^{11} for *C. macrocarpa* [60].

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