ENVIRONMENTAL EFFECTS ON SEED PRODUCTION OF FORAGE LEGUMES

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ABSTRACT

Seed production of forage legumes is a very complicated process with a large number of biotic and abiotic factors involved. There are three principal factors acting and interacting with each other: The plant - the environment - the pollination insects. Maximum seed yields can only be achieved when all of the contributing factors are at their respective optimum. Plant characteristics in relation to seed production include: The genotype; number of plants, stems, inflorescences, florets, ovules, pods; time and length of flowering period; mode of pollination, pollen characteristics, degree of self and cross fertilization; attractiveness to pollinating insects, nectar constituents, volatiles, flower color; development of seeds, seed abortion, seed yield; seed quality. Environmental factors affecting seed production of forage legumes include: Soil characteristics, e.g. type, texture, water, plant nutrients, pH; topography; climate, e.g. photoperiod, light, temperature, amount and distribution of precipitation, air humidity; harmful organisms, insects diseases, weeds. Examples of the effects and interrelationships of certain environmental factors and plant characteristics including the efficiency of pollinating insects from available literature and own investigation are presented and conclusions with regard to the application of available scientific knowledge and further research are drawn.

KEYWORDS

Environment, seed production, forage legumes, plant characteristics, pollination

INTRODUCTION

Seed production of forage legumes may be considered as an ecological system with the main compartments - the plant population - the environment - and the pollinating insects - acting and interacting. Maximum seed yield can only be achieved if the many components of these compartments are at their respective optimums. This, however, is seldom if ever the case. The theoretical seed production potential in lucerne, as an example, is 12000 kg/ha, but the actual seed yield realized even under favorable conditions is only 500 kg/ha or 4% of the seed production potential (Lorenzetti, 1993). So, it is quite logical that the seed producer, by applying appropriate management practices, is trying to optimize the seed production capacity of the plant population e.g. by choosing a high seed-yielding cultivar, by improving the efficiency of the pollinating insects, and by producing the seed under favorable environmental conditions.

In this paper we will first consider the ecological compartments of forage legume seed production in more detail. Then evidence of the effects of various environmental factors on certain plant inherent components within the system of forage legume seed production with examples from pertinent literature is presented. By doing so the relationships between the abiotic environmental factors and plant components will be emphasized, mentioning the effects of pollinating insects only occasionally. Within this context, it is impossible to cover the great number of species of temperate forage legumes in detail. For this reason, lucerne (*Medicago sativa* L.) as a world wide important species, has been chosen as a reference plant.

THE ECOLOGICAL SYSTEM OF SEED PRODUCTION OF FORAGE LEGUMES

Plant inherent factors contributing to forage legume seed yield. An overview of plant inherent factors contributing to forage legume seed yield is presented in Table 1.

Environmental factors affecting seed production of forage legumes. Environmental factors that affect seed production of forage legumes are listed in Table 2 and some characteristics of pollinating insects in relation to seed production of forage legumes are summarized in Table 3.

EFFECTS OF VARIOUS ENVIRONMENTAL FACTORS ON CERTAIN PLANT INHERENT COMPONENTS WITHIN THE SYSTEM OF FORAGE LEGUME SEED PRODUCTION

Genetic population structure. One of the main prerequisites for seed production in forage legumes is to choose a suitable environment; an environment that favors vegetative growth is generally detrimental to sexual reproductive plant development. This situation prevails in most countries in central and northern Europe. Improved management practices can hardly compensate for deficiencies of the environment (Seifarth, 1965). As a consequence, seed production of domestic varieties was increasingly moved to areas with more favorable environmental conditions. For example, the domestic lucerne seed production in Germany in 1995 - 6 ha - was restricted to the production of basic seed to be used for seed multiplication elsewhere. From a practical point of view one should keep in mind that forage legumes are primarily cross-pollinating species and therefore any variety is not a single, well defined genotype but a population consisting of individuals varying within certain limits with regard to their plant inherent components in relation to seed production. If environmental factors such as day length, temperature, precipitation etc. differ significantly between the area of origin and the area of seed multiplication and if, as it has been shown by many authors, genotype-environment interactions within the plant population exist, a genetic shift in the progeny may occur. If this happens, the agronomic value of the forage crop may be affected. The effects of seed production under markedly different environmental conditions have been studied by numerous research workers (Bingefors & Dovrat, 1966; Bula & Garrison, 1962; Panella & Bingefors, 1960; Simon, 1966a; Simon et al., 1974; Smith, 1958; Zaleski, 1962). Simon et al. (1974) concluded that seed of German forage varieties multiplied under the very different environment of California for one generation exhibited neither a significant change of type within progeny nor was the agronomic performance of the progeny adversely affected. In contrast, seed quality was improved as compared to the seed produced in Germany (Simon, 1966a).

Seed yield. The strong environmental influence upon seed yield is stressed by Pedersen & Hurst (1963). Simon (1984) found highly significant differences between replications, positions of replications, and years in a lucerne polycross, indicating a strong environmental effect on seed production.

Soil characteristics. For lucerne seed production soil of limestone origin and loess-covered sand and gravel soils are particularly well suited (Lampeter, 1982). The paramount soil characteristic, however, is the water status during the growing period. Mean soil moisture suction pressure between 2 and 8 bars is optimum for lucerne seed production provided the soil is kept continuously moist until time of blossoming, and irrigation water is not applied during the period of heavy bloom (Taylor et al., 1959). Irrigation requirements are dependent upon soil texture and depth, natural precipitation, temperature, length of growing season, and cropping practices (Pedersen et al., 1972). Highest seed yields are obtained when irrigation practices prevent severe plant stress and promote slow, continuous growth through the entire production period without excessive stimulation of vegetative growth (Rincker et al., 1988). High water rates decrease seed yields; a moderate rate, applied at mid-flowering to a relatively dry soil, markedly increased seed yield (Goldman & Dovrat, 1980). Most forage legumes require an ample supply of soil-P, -K, and -Ca, with the soil-pH not below 5.8-6.0 (Lampeter, 1982). However, in lucerne, the application of fertilizers has not increased seed yields except where severe localized deficiencies have existed (Pedersen et al., 1972). Stjepanovic et al. (1990) found favorable effects of the application of micronutrients (B, Mo, Zn, Mn) with seed yield increases of 21-27% (B), 10-39% (Mo), 12-21% (Zn), and 0-26% (Mn) relative to the untreated control.

Topography. The topography of the vicinity around the seed production field is important for the establishment and activity of wild pollinators. Relatively small fields encompassed by landscape structures that favor wild bee activity may benefit ample pollination. Simon (1984) found highly significant differences in seed setting relative to the exposition to the nesting sites of bumble bees and honey bees.

Climate. The greatest part of variability in lucerne seed yields is due to climate variability (Lorenzetti, 1993; Djukic et al., 1993; Simon, 1984). Seifarth (1965) and Simon (1966b) found highly significant positive correlations between lucerne seed yield and average temperature and duration of sunshine but negative correlation with air humidity, cloudiness, number of rainy days, and amount of rain in the month of July (Table 4).

Lorenzetti (1993) describes an ideal weather regime during the growing season as follows: "After a period in which induction and initiation requirements are satisfied, seed production requires moderate and well-distributed rainfall during the vegetative growth period in spring and early summer, a spell of fine weather at the time of pollination followed by a gentle rain during the filling of the seed and a dry and sunny period for ripening and harvesting."

Temperature is another important climatic factor influencing lucerne seed production. According to Dotzenko et al. (1967) temperature during the period from forage removal to full bloom appeared to have the strongest influence on seed produced, i.e. the greatest reduction in seed yield occurred when maximum and minimum temperature were highest. But generally high temperatures combined with low humidity are recognized as favorable for seed production (Myers, 1959; Seifarth, 1965; Simon, 1966a; Staszewski, 1996). Cressman (1963) found temperatures between 14ºC and 20ºC most favorable for seed production in self-fertile lucerne clones. Seed yield decreased with increasing temperature from 21ºC to 29ºC. The optimum temperature for seed maturation is between 27ºC and 32ºC (Blondon & Guy, 1974).

Low air humidity is generally regarded as favorable for seed production (Myers, 1959; Seifarth, 1965; Simon, 1966a). Jablonski (1973) found relative humidity of 50-60% the most favorable in lucerne.

A great number of *harmful organisms* may adversely affect forage legume seed yields. These include insects, diseases and weeds. Insect damage has been reviewed by App & Manglitz (1972). Weeds reduce yields, slow harvesting and increase cleaning costs (Pedersen et al., 1972).

ENVIRONMENTAL EFFECTS ON SELECTED YIELD COMPONENTS.

Number of plants and stems. The number of plants and stems per unit area is primarily determined by the seed rate and cultural practices. Increasing moisture stress reduces the number of stems (Fick et al., 1988). Increasing the temperature from 16ºC to 32ºC decreased the number of stems (Simon, 1958).

Number of inflorescences. The number of inflorescences per stem is decreased under moisture stress conditions (Fick et al., 1988). Temperature, particularly during the period from forage removal to full bloom, appeared to have the greatest influence on the number of racemes per stem in lucerne (Dotzenko et al., 1967). Guy et al. (1971) observed that over the 17ºC to 27ºC temperature range increasing temperatures generally increased the number of racemes per stem at the expense of number of flowers per raceme. The number of racemes was considerably reduced under high temperature (32ºC), and temperature x genotype interactions were evident according to Simon (1958). Cressman (1963) found no apparent effect of temperature on raceme formation.

Flowering. Competition between vegetative and reproductive growth for available photosynthate is one of the basic factors affecting flowering and seed production. When environmental factors favor vegetative growth, few flowers are produced (Bula & Massengale, 1972). Processes associated with floral initiation and development are markedly influenced by temperature (Bula & Massengale, 1972; Staszewski, 1996). But there is conflicting evidence relative to the effect of high temperature on flowering. In lucerne, Nittler & Kenny (1964) reported an average percentage of flowering plants of 51, 81 and 89 at 30, 27 and 24ºC, respectively. High temperature (32ºC) partially inhibited the ability to flower (Simon, 1958). The time required for flower initiation decreased as the average minimum temperature increased (Dobrenz et al., 1965). Guy et al. (1971) concluded that the effect of temperature on flower number is complex. Over the 17ºC to 27ºC range, the number of florets per raceme decreased. High temperature also reduces considerably the flowering period and the time from tripping to mature seeds (Simon, 1958).The number of florets is very much dependent on daylength during flower initiation. Most temperate forage legumes are long-day plants. The change from vegetative to reproductive development requires repeated exposure to appropriate photoperiodic cycles (Massengale & Medler, 1958). Lucerne flowers most profusely when exposed to continuous light (Nittler & Kenny, 1964). The influence of photoperiod on flower initiation is altered by temperature (Massengale et al., 1971). Lucerne plants growing under short days at 12ºC produced flowers, but not at 17ºC. At this temperature, plants flowered only under long days (Roberts & Struckmeyer, 1939). The authors conclude that when considering the photoperiodic requirement of lucerne it is important to consider the influence of temperature during the induction and initiation periods. Simon (1958) observed a very different response of lucerne genotypes when daylength was reduced from 16h to 12h, thus having a strong indirect effect on seed setting. This is also evidence for the possibility of a genetic shift within a lucerne population when multiplied under shorter daylenghts. Furthermore, the light intensity required for floral induction is relatively high (Nittler & Kenny, 1964).

Pollination. The flowers of forage legumes are adapted to pollination by insects. In fact, fertilization and seed setting in most species depend on preceding cross-pollination. One of the exceptions is lucerne, which is predominately cross-fertile but with various degrees of self-fertility. Since the activity of pollinating insects is strongly influenced by the prevailing weather conditions during the flowering period, pollination is affected by the environment via insect activity. In lucerne, cross-pollination occurs only when the flower has been tripped.

Tripping is understood as the sudden release of the sexual column from the keel of the flower where it is held under pressure within the two keel petals. When the petals are parted, the sexual column snaps forward until it comes to rest on the standard petal of the floret. Tripping is effected by mechanical pressure applied by pollinating insects and influenced by environmental factors such as wind, rain, heat, and cold (Viands et al., 1988). The necessity of tripping as a prerequisite of pollination and seed set is generally accepted. But seed setting without tripping has frequently been observed. Under certain climate conditions in the field, fertilization and pod set have been observed to occur in the untripped flower (Barnes et al., 1972; Myers, 1959). High temperatures combined with low humidity are generally recognized as favorable for tripping (Brink & Cooper, 1936; Knowles, 1943; Myers, 1959). High temperature and low humidity are effective in fostering tripping indirectly by increasing insect activity and possibly by making the plants more attractive to pollen collectors.

Pollination is affected by temperature (Bula & Massengale, 1972) and air humidity (Staszewski, 1996). Masslinkow (1956) regards temperatures from 25-34ºC and relative air humidity from 30-60% as optimal.

Pollen characteristics. Pollen quantity and quality may be affected by environment (Lehman et al., 1969). The proportion of viable pollen is an important characteristic in both male-fertile and male-sterile lucerne plants. Pollen viability has been shown to be strongly influenced by environmental factors such as daylength, temperature and light. Temperature had a much greater effect with 30% more sterile pollen from plants grown at 15ºC than from plants grown at 24/19ºC in male-sterile plants (Suginobu & Maki, 1979). The percentage of viable pollen was significantly greater in 12 hours daylength than in 16 hours, and at 32ºC as compared with 16ºC (Simon, 1958). Also Blondon et al. (1979, 1981) observed increasing pollen number and fertility with increasing temperature from 17ºC to 27ºC. Pollen grain size, germination and tube growth varied significantly with sampling dates through the growing season indicating a strong environmental effect upon these characters (Lehman et al., 1969). Clones evaluated for *in vitro* pollen growth characteristics showed highly significant differences among temperatures and for clone-environment interactions (Straley & Melton, 1970).

Self fertilization. The degree of selfing may be affected by temperature and humidity (Pedersen et al., 1972; Veronesi et al., 1988). Highly significant differences for self-fertility among temperatures (16, 21, 27, 32ºC) were observed by Straley & Melton (1970).

Attractiveness to pollinators. Nectar, odor and flower color are characters that have been shown to be associated to attractiveness of flowers to pollinating insects. Factors affecting nectar yield include heredity, flower size, sunshine, moisture, and soil fertility (Pedersen et al., 1972). Nectar quality may also affect bee visitation. The sugar content of the nectar is influenced by the plant and the environment, with atmospheric humidity being the dominant factor.

Odor was assumed to be the major factor in clonal preference by individual honey bees (Boren et al., 1962). The production of volatiles reached a maximum 6 to 8 hours after the beginning of the light period, and decreased to almost nil at 11 hours after the beginning of the illumination (Loper & Lopioli, 1972). With regard to flower color, honey bees prefer blue- and purple-flowered over white- and yellow-flowered plants (Kehr, 1973).

Pod formation. The percentage of flowers setting pods may vary considerably, depending upon the environment (Tysdal & Kiesselbach, 1944; Viands et al., 1988). Both high and low water supply reduce pod set (Fick et al., 1988). Relative humidity above 50 % also appeared to reduce pod set, especially at high temperature (Grandfield, 1945). A significant variability with respect to pod number per inflorescence between years reflects a strong influence of the prevailing weather conditions (Djukic & Kraljevic-Balalic, 1993). The percentage pods set was significantly greater at low temperature (16ºC) than at high temperature (32ºC) (Simon, 1958). The highest percent pod setting within ranges of temperature from 20-32ºC and relative humidity from 44-84% occurred at 28ºC and 44% (Mistinova, 1984). No apparent effect of temperature on pod set was observed by Cressman (1963).

Seed characteristics. An effect of weather conditions on seeds per pod is suggested by Djukic & Kraljevic-Balalic (1993). The number of seeds per pod is markedly influenced by temperature, i. e. reduced at high temperatures (Dotzenko et al., 1967). Jablonski (1973) regards as the best condition of seed setting when air temperature is between 25-35°C and relative humidity 50-60 %. Severe moisture stress reduces the number of seeds per pod (Fick et al., 1988).

For seed maturation the optimum temperature is 27-32ºC (Blondon & Guy, 1974). Unfavorable weather conditions during this period may cause seed abortion or pod abscission. Dane & Melton (1973) reported that the amount of seed abortion nearly doubled between 27ºC and 32ºC.

It is generally accepted that environmental effects particularly during the period of seed ripening can strongly influence seed quality. The percentage of hard seeds is governed by edaphic and climatic factors during and after seed maturation. The same cultivar grown in different environments may exhibit wide variations in hard-seed content (Gunn, 1972). Severe moisture stress increases the hard-seed percentage and the 1000-seed weight (Grandfield, 1945).

Lucerne seed of the same origin produced in Germany and in California had a 1000-seed weight of 2.02 and 2.35 g, respectively, and the percentage of hard seed of 26 and 2 %, respectively (Simon, 1966a). Also the time from seeding to field emergence was 3 days shorter in the California provenance indicating an overall beneficial effect on seed quality when seed of German origin is produced under climatic conditions similar to those prevailing in California.

CONCLUSION

Forage legume seed production may be regarded as a complex ecological system with three main compartments - the plant population, the environment, and the pollinating insects - acting and interacting. Average seed yields achieved in commercial seed production are far below the theoretical seed production potential. This is mainly due to the suboptimal expression of environmental factors.

The influence of various environmental factors on seed yield in general and on components of seed yield has been studied and reported by a great number of scientists over an extended period of time. The results present convincing evidence of the action and interaction of the environment on components of seed yield and seed yield itself in forage legumes. The knowledge derived from pertinent research can be used for recommendations how to improve forage legume seed yield by applying appropriate environment-related management practices.

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Table 1
Plant inherent factors contributing to seed production of forage legumes

Genotype, Population structure	Pod formation
Plant morphology	Seed
Plants per unit area	Development
Stems per plant	Fertilization of ovules, proportion
Inflorescences per stem	Abortion
Florets per inflorescence	Abscission and detoriation
Ovules per ovary	Number or weight of seed per unit area
Pods per plant etc	= YIELD
Seeds per pod etc	
Pollination	Quality
Pollen	1000-seed weight
Amount	Germination
Viability	Hard seed
Tube growth	Contamination
Self-fertility,-sterility	
Attractiveness to pollinating insects	
Nectar	
Amount, Availability	
Chemical composition	
Volatiles	
Intensity	
Chemical composition	
Flower color	

Table 2
Environmental factors affecting seed production of forage legumes

Soil	Climate
Origin	Photoperiod
Texture	Light intensity, quality
Depth	Temperature
Water	Precipitation amount, distribution
Plant nutrients	Air humidity
pH	Air flux
	Length of growing period
Topography	
	Harmful organisms
	Animals, Insects
	Disease
	Weeds

Table 3
Pollinating insects in relation to seed production of forage legumes

Species	Number
Honey bee	Efficiency
Bumble bee	
Leaf cutter bee	
Alkali bee	
Other	

Table 4
Relationship between lucerne seed yield and climate factors in July

Seed yield	no. years	rain % of average	no. rainy days	average temperature ºC	sunshine h	relative humidity %/14^{20}h
a) good	9	60	10	19.7	285	47
b) intermediate	14	124	16	18.0	235	55
c) poor	6	137	16	17.4	199	60
significance						
a : b		**	**	**		**
a : c		**	**	**	**	**

** P < 0,01