Theor Appl Genet (1984) 68 : 1–9

© Springer-Verlag 1984

The lupin – ancient and modern crop plant *

W. Hondelmann

Institut für Pflanzenbau und Pflanzenzüchtung, Bundesforschungsanstalt für Landwirtschaft Braunschweig-Völkenrode (FAL), Bundesallee 50, D-3300 Braunschweig, Federal Republic of Germany

Received December 28, 1983; Accepted January 16, 1984
Communicated by H. F. Linskens

R. von Sengbusch

What would be more suitable to discuss in a lecture in honour of Reinhold von Sengbusch than that research project that brought him early and permanent fame, i.e. the lupin. This crop plant brought him *early* fame because it was the first and most important of a series of plant species domesticated by him before World War II. It brought him *permanent* fame because it has become the classical example of successful domestication on the basis of simple Mendelian inheritance. This is evidenced in textbooks at home and abroad. At the same time, the alkaloidfree "sweet" lupins, which were selected for in the course of his early research work, ultimately proved to be one of the first experimental records of the "law of homologous genes" that was postulated by the Russian geneticist Vavilov a few years ago.

The genus *lupinus,* comprising more than 300 species, is a large one, but only few species achieved an agricultural importance. These are the 'Old World'-species *L. albus,* white lupin, *L. luteus,* yellow lupin, and *L. angustifolius,* narrow-leafed or blue lupin – all of which originate in the Mediterranean area. One 'New World'-species, *L. mutabilis,* the Andean lupin from South America, also belongs to this group. The genus, therefore, is comprised of geographically separated centers of diversity (Fig. 1).

An impression of these species is presented by the following illustrations. The first two are taken from the "Kreutterbuch" of Matthiolus (Frankfurt 1586). They exhibit, using pre-Linnean nomenclature, *L. albus* (Fig. 2), which at that time was cultivated, and the wild species *L. luteus* and *L. angustifolius* (Fig. 3). Contrast these old paintings to a photograph of a field of *L. mutabilis* growing at an altitude of about 3,000 m near Cusco/Peru (Fig. 4).

* Lecture given on the occasion of awarding a honorary doctor's degree to Prof. Dr. R. von Sengbusch at the University of Giessen on November 25, 1983

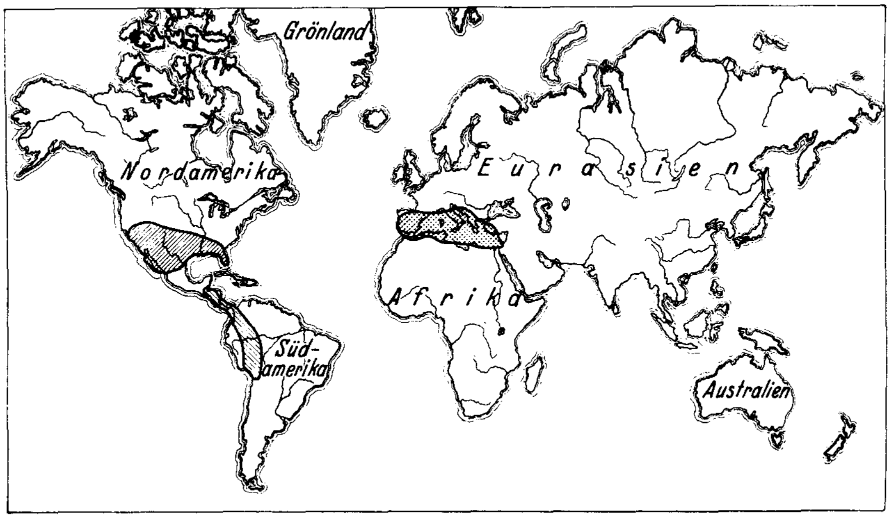

Fig. 1. Centers of diversity in the genus *Lupinus* (from v. Sengbusch 1935)

Fig. 2. *L. albus* (from Matthiolus 1586)

Fig. 3. *L. luteus* and *L. angustifolius* (from Matthiolus 1586)

The lupin, in its evolution from a wild to a crop plant, had an eventful history that was accompanied by periods of both booms and declines even though it showed evidence of being multi-purposal. In the first place, it is a plant for green manuring on account of its capacity to fix nitrogen from the air and to dissolve phosphorus and other minerals in the soil. It is also a fodder crop which because of its content of alkaloids can be used only to a limited extent. Its seeds can be used on an unlimited scale after rinsing away these

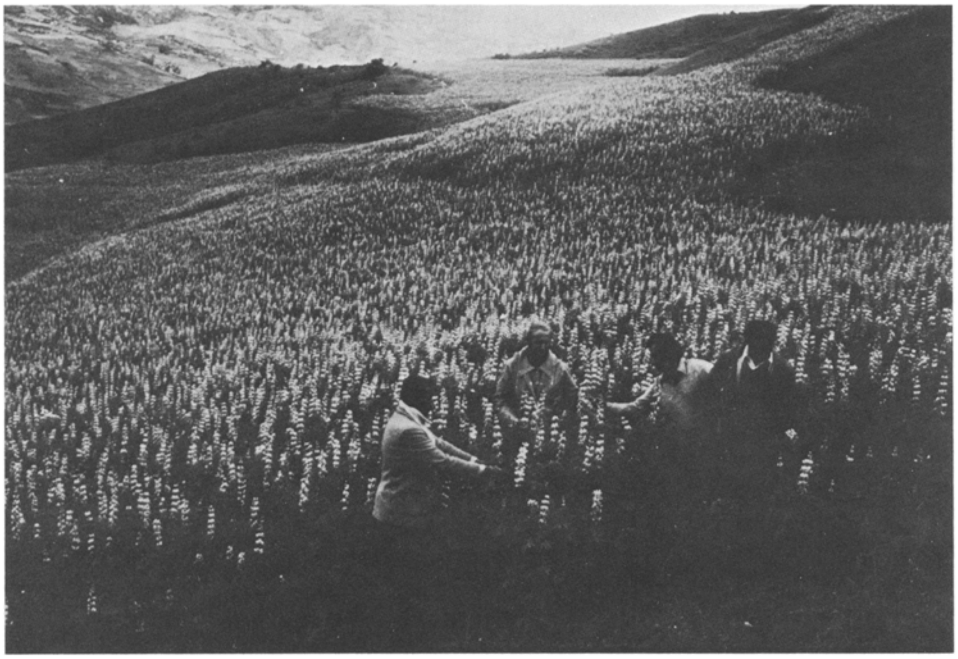

Fig. 4. *L. mutabilis* in the Andes

toxic constituents. Finally, the alkaloidfree types are first-rate grain legumes due to the high protein and oil content of the seeds.

Thus, it is fascinating to look at the old and new crop plant from two different perspectives – first from the historical, and second from the scientific one, dealing with plant breeding.

To start with the historical point of view: The old crop plant is represented by two species, *L. albus* and *L. mutabilis.* The first one, which is probably presented by its subspecies *termis,* was evidently grown in old Greece and presumably in the Nile valley as well; the later in the pre-Columbian civilizations of the South America Andean regions.

Documents show that the cultivation and uses of white lupin were known to the ancient Greeks. The well known physician, Hippocrates, from Kos (400–356 B.C.), and above all, Theophrastus, philosopher and naturalist (372–288 B.C.), in his "Historia plantarum" discuss the species in detail. Theophrastus writes in a passage that "it likes more sandy and poor soil, but will not grow at all on cultivated land", and in another passage he writes: "... which must not be harvested before rain, because (the pods) are dehiscent and grains are dispersed." Demands on soil type as well as the problems raised by dehiscent pods were well known at that time.

The same applies to the old Roman literature. The feeding of lupins to cattle is mentioned several times. Among the authors are the elder Cato (243–149 B.C.), rigid censor as well as experienced farmer, who numbers it among those crops "which manure the seed", and Varro, the most learned writer in the period of revolution. Virgil, the great epic poet of the Augustean era, speaks in high terms of the lupin in his famous rural didactic poem, the Georgica:

"Aut ibi flava seres, mutato sidere, farra
nude prius laetum siliqua quassante legumen
aut tenuis foetus viciae, tristisque lupini
sustuleris fragiles calamos, silvamque sonantem."[1]

Disregarding the poetic quality of these hexameters and the significance of the Georgica on the whole, there is a very practical sentence to be found, which is: white lupins and also vetches are grown as a preceding crop in rotation with cereals.

Mentioning only the most important writers of the first century A.D. who describe lupins, white lupins are quoted in Columella's popular book, "De re rustica", in Dioscorides' textbook of pharmacology, "De materia medica", a classical textbook for more than one millenium, as well as in the elder Plinius, multi-volumed compilation "Naturalis historiae libri".

All ancient writers emphasize that the lupin is able to grow on poor and barely arable land and to improve it. In 218 A.D. Florentinus reports on debittering the seeds in the same way as it is done nowadays in primitive agricultural systems, i.e. to dip bags filled with grains into running waters.

[1] Or else, changing the seasons, put down to yellow spelt,
A field where before you raised the bean with its rattling pods
Or the small-seeded vetch
Or the brittle stalk and rustling haulm of the bitter lupin
(Translated by C. Day Lewis, London 1974)

In the German literature lupins are first recorded as "Feigbohnen" by Hildegard of Bingen in the 12th century. There is no indication that knowledge of this plant had been improved on since ancient times. Until the late Middle Ages this remained the state of development as it can be seen from the herbals of that time.

Early documents on the Andean lupin are scarce. Archaeological findings to which a date could be assigned are the basis of our knowledge on cultivation and use. The cultivation of lupins as early as the 6th and 7th century B.C. could be established. Later on, in the zenith of the Nazca (100–800 A.D.) and Tiahuanaco civilizations, it was regularly used in crop rotation. Subsequent references indicate a similar development to the one the white lupin went through in Southern Europe. Garcilaso de la Vega, a late witness of the Spanish conquista, reports about 1600 A.D.: "They (the Incas) also have lupins as we have in Spain, but somewhat larger and whiter, they are named tarhui." Conversion to the Spain traditional methods in agriculture and changes in taste of the indigenous civilization occurred gradually through the centuries. The importance of the lupins decreased and only marginal locations in extreme altitudes survived even though the high nutritive value had been known for generations and, therefore, methods of debittering the seeds were in use.

In the 18th century the cultivation of lupin in Europe expanded. Evidence is given of this by two passages in letters. The first is dated from February 17th, 1781, and runs as follows:

"Mein lieber Etats-Minister Michaelis. Dieses Jahr zahle ich alles ab, was von Meliorations aufgesetzt gewesen usw. Sodann mache ich Euch vorläufig bekannt, daß ich einen Samen namens Lupin aus Italien kommen lasse, daraus wächst ein Kraut, ongefehr wie Erbsen, das erste Jahr ist es damit weiter nichts, das andere Jahr denn wird das Land mit samt dem Kraut und allen was drin ist, umgepflüget, und das prätendieren sie in Italien, daß das ebensogut und fett seyn soll, wie der Dünger. Friedrich"[2].

No less a person than Frederick the Great became involved in introducing the lupin into Prussia (as he did with several other crops). He continued his correspondence to the same minister on March 21st, 1781: "Wegen des Lupins kommt es darauf an, zum ersten, daß man weiß, wie es in Italien gemacht wird. Nämlich das Land, das nur schlechtes Sandland sein muß, wird einmal umgepflügt und nicht gemistet, dann wird der Lupin darein gesäet; daraus wächst dann ein Kraut, ongefehr wie von Erbsen, das zeug ist jedoch nichts nutze, weder zum essen noch vor das Vieh, sondern wenn es reif ist, schneidet man es ab und läßt es auf demselben Fleck liegen und verfaulen; hier muß man es länger liegen lassen, daß es recht verfaulet, denn umso besser düngt es dann das Feld. Zum anderen, wenn es dann verfaulet ist, das Kraut, so wird solches das andere Jahr wieder untergepflügt und das gibt dem Land den Dünger. Wenn denn dieses Kraut verfault und untergepflügt ist, so wird das Land besäet und trägt das denn auch gut. Nun ist meine Idee, daß wir das 4- und 5-jährige Land dazu gebrauchen wollen, und um den Nutzen davon zu sehen, wollen wir zwei Proben auf solchen mit Lupine gedüngtem Land machen: auf eine Art, daß wir Roggen, Gerste und Hafer darin säen, und auf die andere Art, daß wir das mit Luzerne probieren, damit wir sehen, wie solches am besten gerät".[3]

However, these efforts had no lasting success. After the death of Frederick the interest of the state authorities decreased and the cultivation of lupin declined. Elisabeth Schiemann, who published these letters, which were kept in the Prussian State Archives, noticed correctly that it was the selection of *white* lupin which contributed largely to the unsuccessful acclimatization. A few decades later the *yellow* lupin spread very fast without any support from state agencies. The ideas of Frederick the Great apparently survived. In 1817 a farmer, v. Wulffen, experimented anew with white lupin, again without convincing success. Even the efforts of the economic councillor Kette proved insufficient. He turned to *L. luteus* when another farmer, Borchard in the Altmark, demonstrated that this species was the better adapted one for green manuring on account of its more uniform and safer ripening.

About 1860 cultivation of the bitter yellow lupin was widespread on the sandy and more acid soils of North German lowlands. *L. luteus* was not only used

[2] "My dear Secretary of State Michaelis. This year I'll pay off all that has been put into action by meliorations, etc. Then I will aquaint you of the fact for the time being that I have sent for a grain from Italy named lupin. From this a herb is growing about that of a pea. In the first year it is nothing, in the second year the land can be ploughed, including the herb and everything in it. In this way they take care of it in Italy, and this should be as good and rich as is manure. Frederick"

[3] "Regarding the lupin it is the main point at first that one knows, how it is being done in Italy. That is, the arable land, which has to be poor sandy soil only, has to be ploughed once and not manured, then the lupin is sown. From this a herb is growing about that of a pea. But the stuff is not good at all, neither for food nor for cattle. But when mature it is cut and remains on the spot for rotting. Here it must be left for some time because the better the rotting, the more its manuring effect on the field. Second, when it is moulded, the herb, it is turned under, and this provides the manure for the soil. When this herb is moulded and turned under, sowing is being done, and the field will produce a good yield. Now it is my idea that we should try four of five year old fields for this, and, in order to see the benefit from it, we will make two experiments using fields manured by lupins: the first, to sow rye, barley and oats in it, and the second to try it with alfalfa in order to learn how it turns out to be successful"

for green manuring but also for feeding sheep, preferably using the seeds. The economic councillor Schultz-Lupitz participated decisively in this success. He published in 1881 a brochure "Der Zwischenfruchtanbau auf leichten Böden" (Intercropping on light soils), which soon became a catechism for lupin growing. The blue lupin, *L. angustifolius,* also seems to have been introduced in these years.

Set-backs did not fail to appear. In the second half of the seventies severe pathological symptoms were observed repeatedly in those sheep which had been fed with bitter lupin grains for a longer period. This disease called lupinosis proved fatal in many cases. A drastic decline in cultivating grain lupins was the result. Nevertheless, the acreage stabilized at about 400,000 ha, 100,000 ha of which were used for harvesting grain lupins.

Soon after 1900 sheep husbandry had a severe recession caused by the import of cheaper wool from abroad. Moreover, the competition of mineral fertilizers did more than was necessary. Thus, cultivation of lupins was decreased again. It was only in times of emergency, World War I and the following years, that a new expansion followed as a result of the protein shortage in Germany. To stimulate the interest in lupins no effort seemed to be too great. In October 1918 the Association of Applied Botany was invited to a lupin dinner. There, on a table-cloth made of lupin fibers, a lupin soup was served followed by a lupin steak fried in lupin oil and spiced with lupin extract. In addition, lupin margarine containing 20% of lupin constituents, cheese from lupin protein, lupin spirits and lupin coffee were offered. Moreover, lupin soap for washing hands, paper and envelopes supplied with lupin adhesives were available.

Irrespective of this, the interest in lupins free from alkaloids which could be used as high-grade grain legumes, was steadily increasing. In 1910 Fruwirth published in his textbook "Die Züchtung der landwirtschaftlichen Kulturpflanzen" the following sentences: "Bei Körnernutzung wird der Wunsch nach einer Lupine, die arm an Alkaloiden ist, geäußert. Es ist mir nicht wahrscheinlich, daß man auf dem Wege der Veredelungszüchtung mit Massenauslese zu einem bezüglichen Erfolg gelangen könnte, der nennenswert wäre, und eine geringe Drückung des Ertrags hätte keinen Wert. Für einen Schluß auf den Alkaloidgehalt der Körner von anderen Eigenschaften aus sind keine Grundlagen vorhanden, und eine Bestimmung des Gehaltes ist pflanzenweise nicht durchzuführen, da eine überdies schwierige Alkaloidbestimmung größere Mengen Samen erfordert".[4]

Fruwirth (1910) and Roemer (1916) also discussed the production of species hybrids in order to solve this problem.

At this point I will quote our distinguished honorary doctor. Dr. von Sengbusch writes: "Seit der Jahrhundertwende haben sich verschiedene Forscher mit der theoretischen Möglichkeit der Schaffung alkaloidfreier Lupinen (Süßlupinen) beschäftigt. Es erhebt sich die Frage, wer erstmalig den Gedanken gehabt hat, daß es möglich sein müsse, auf dem Wege der Auslese zu bitterstoffreien Formen zu kommen. v. Rümker (1913), Roemer (1916), Wittmack (1921), Pryanishnikov (1924) und Baur (1927) hatten aufgrund der Erkenntnisse der Vererbungsforschung, insbesondere wohl der Mutationsforschung das Vorkommen alkaloidfreier Mutanten vorausgesagt. Roemer hat dadurch, daß er an die Lösung des Problems heranging, bekundet, daß er die Aufgabe für lösbar hielt".[5]

He continues:

". . . haben v. Arnim, Claassen und Roemer sich als erste praktisch mit der Auslese alkaloidarmer Lupinen beschäftigt. v. Rümker (1913), Roemer (1916) und Wittmack (1921) haben auf die Notwendigkeit einer Linien- bzw. Einzelpflanzenauslese zum Zweck der Auffindung alkaloidfreier Formen hingewiesen und den Züchtern nahegelegt, sich damit zu beschäftigen. Somit dürfte v. Rümker der erste gewesen sein, der die Auslese alkaloidfreier Lupinen für möglich gehalten hat".[6]

The reason why such a genotype had not yet been detected, even more, could not be detected, was that no suitable analytical method was available to determine the alkaloids.

---

[4] . . . Textbook "Improvement of agricultural crop plants": . . . "For using the grains request has being expressed for a lupin, which is poor in alkaloids. It does not seem probable to me to succeed in this to any extent by plant improvement through mass selection. A slight decrease in yield would be of no value. There is no evidence to conclude from other characteristics as to the alkaloid content of seeds, and a determination of alkaloids cannot be done by use of single plants, since this determination, which is a laborious one, requires larger quantities of seeds"

[5] "Since the turn of century several research workers have been concerned with the theoretical possibility of developing alkaloidfree lupins (sweet lupins). The question arises, which person at first hit upon the idea that it must be possible to develop alkaloidpoor types by means of selection. v. Rümker (1913), Roemer (1916), Wittmack (1921), Pryanishnikov (1924) and Baur (1927) predicted the occurrence of alkaloidfree mutants in virtue of knowledge in genetics preferably of mutation research. Roemer by making an approach to solve the problem had manifested that he considered it to be solvable"

[6] "v. Arnim, Claassen and Roemer were the first to try to select alkaloidfree lupins in practice. v. Rümker (1913), Roemer (1916) and Wittmack (1921) pointed out the requirement of selecting lines or single plants in order to detect alkaloidfree types. They suggested that plant breeders should get concerned with that problem. Thus, v. Rümker could have been the first to consider it possible to select for alkaloidfree lupins"

I quote Dr. von Sengbusch again:

"Baur (1927) hat dann in derselben Vorlesung, in der er von der Wahrscheinlichkeit des Vorhandenseins alkaloidfreier Mutanten sprach, ausgeführt, daß allein eine geeignete Schnellbestimmungsmethode für Alkaloide für die Lösung des Problems entscheidend sei.

Ich selbst habe 1925 die russische Arbeit von Prianischnikow für Roemer übersetzt und wurde hierdurch erstmals auf das Problem der Züchtung alkaloidfreier Lupinen hingewiesen. Aber erst in der Vorlesung von Baur, in der er über die Möglichkeit der Lösung und über die Bedeutung des Lupinenproblems sprach, wurde in mir der Wunsch wach, mich mit diesem Problem zu beschäftigen".[7]

This summary of the previous history of the sweet lupin was published in 1942, 14 years after these experiments had been conducted. The publications summarizing all results and methods connected with these experiments were subjected to a period of closure. The papers had to be given in trust to the Kaiser-Wilhelm-Gesellschaft in Berlin, a demonstration of the economical importance which had been awarded to this research work.

The situation concerning the four lupin species in question just before v. Sengbusch started his work is shown in Fig. 5 (taken from one of his publications in 1947). It contains an arrangement of those wildtype characteristics which are essential to differentiate the wild lupins from cultivated ones. The old crop plants, *L. albus* and *L. mutabilis,* exhibit the character expression desired with the exception of alkaloid content. On the other side, *L. luteus* and *L. angustifolius* (with the exception of 2 characters of the latter one) do not demonstrate this, i.e., the old agricultural people were able to select for visible traits but not for invisible ones like metabolic products.

The crucial perception was that boiled seeds, later on only soaked, in water dissolve the alkaloids but not other N-containing substances. After application of a few drops of a iodine-mercury-potassium iodide solution a white precipitation is formed.

This quick-method, which was refined in the following years due to the special conditions of the different species, became an often unmatched model as an analytical tool for plant breeders. By means of the new method the first sweet grains of *L. luteus* could be selected for during the winter 1927/28 in Berlin-Dahlem. The following summer, now at Münneberg, three plants of that species could be selected using a method adapted to leaf analyses. These became the original plants of lines 8, 80 and 102, which were basic material for all German and foreign cultivars of a yellow lupin.

In the same way selection for *L. angustifolius* was accomplished. During the winter months 1928/29 the first sweet grain was detected, two plants in the following season. After having solved the next essential problem – obtaining plants of *L. luteus* with non-shattering pods – in 1935, the next phase in evolution, the stage of a food crop plant, according to v. Sengbusch, had been reached.

Sweet mutants in other lupin species were selected for thereafter, also in *L. mutabilis.* Genotypes having permeable seed coats and white seeds completed the gene pool of the new lupins. The non-shattering trait of *L. angustifolius* proved to be unstable. It was as late as the 1960's, in Australia, that this objective was finally achieved. Under the designation "v. Sengbuschs Müncheberger Gelbe Grünfutter-Süßlupine" and "v. Sengbuschs Müncheberger Blaue Grünfutter-Süßlupine" the first alkaloidfree cultivars of the lupin were released in 1933 and 1934, respectively. The acreage, originally a multiplication plot of 2 ha increased to 111, 103 in 1938.

The history of lupin became the history of sweet lupin.

L. albus, the most critical of the three European species subsequently was bred as an oil crop first by v. Sengbusch and then by other breeders. But looking at the thing at a whole, it has to be stated that a success comparable to that of *L. luteus* and *L. angustifolius* could not be achieved, not even at that time when mutants with a shorter growth habit and earlier ripening date were available. Experiments to establish species hybrids were attempted as well.

Meanwhile, breeding work had started in Poland. This country developed into a leading lupin producer. There, as in other Central and Eastern European countries, the cultivation of yellow and blue lupins dominated, whereas the white lupin spread over Southern Europe.

What had happened to the Andean lupin in that period, which was the most successful of the European species? Even though its nutritive value was known for centuries, it remained restricted to small and scattered areas. Since at all times the history of plants cultivated by man is part of the history of civilization, it has to be pointed out that parallel to the stagnation of growing lupins in the Andean region, the fate of the old Andean

[7] "Baur in 1927 pointed out in the same lecture, in which he spoke about the probability that alkaloidfree mutants would exist, that only an appropriate analytical method by means of which alkaloids could be screened would solve the problem. In 1925 I myself had translated the paper of the Russian research worker Pryanishnikov in which I came across the problem of breeding alkaloidfree lupins. But it was as late as the lecture of Baur, in which he pointed out the importance of this problem in lupins and discussed possibilities of solving it, that I became filled with the desire to be occupied with that problem"

civilized nations is reflected: these civilizations were superseded and vanished.

After 1945 an altered scenerio can be observed. Other countries and continents introduced the lupins as a crop plant. Above all, Western Australia, New Zealand and South Africa with its Cape province were evolving into new centres of lupin growing. In the Mediterranean area some countries were promoting the cultivation. In our own country, as a result of World War II and the separation of the former German State into two smaller states, lupin growing on the territory of the Federal Republic of Germany, which was not a typical lupin growing area, was not longer of any importance. On the other hand lupins maintained or even increased their part of arable land in parts of the GDR, especially in Poland and in the Soviet Union. Altogether, more than 1.5 million ha are being grown in Eastern Europe, a most notable dimension.

A broadly based breeding programme for *L. angustifolius* started during the 1950's in Western Australia and resulted in the first non-shattering cultivar by I. S. Gladstones in 1967. Due to the initiative of E. v. Baer, alkaloidfree forms of *L. albus* and *L. luteus* could be established in Chile. The same species played an important role in a long-running project of German technical aid in Peru in order to improve protein and fat supply. Moreover, an interest in the native Andean lupin was created with respect to cultivation as well as to breeding programmes. Our colleagues of the University of Giessen were engaged in studying nutritive problems under this programme. If only the debittering had been operating on a larger technical scale or alkaloidfree varieties had been available, the total area of 5,000 ha planted during the project period would have been exceeded by far.

Nevertheless, the revival of lupins in South America can be taken for granted. On a world wide scale the trend of development is also climbing. Will this trend continue or do we have to expect another decline? The answer to this question depends primarily on further progress in breeding.

The aspects connected with these problems can now be discussed. The initial situation v. Sengbusch came upon when starting his experiments, is shown in Fig. 5. The inheritance of these characters, which are the most essential ones for domesticating the wild lupin, followed simple Mendelian segregation. Up to now more than 50 of those major genes have been analyzed. Until the 60's searching for such genes and analyzing their mode of inheritance was a substantial part of experiments with lupins. That is, qualitative characteristics were investigated for. Meanwhile plant breeding evolved into a more quantitatively orientated way of thinking which also affected the approach to research work on lupins.

Characteristic	*L. luteus*	*L. angustif.*	*L. albus*	*L. mutab.*
Alkaloid content	–	–	–	–
Shattering pods	–	–	+	+
Shedding pods	–	–	+	+
Non-permeable seed coat	–	–	+	+
Slow early growth	–	+	+	+
Dark seeds	–	–	+	+
Hairiness	–	+		+

(– = negative expression, + = positive expression)

Fig. 5. Wildtype characteristics of lupin species, when von Sengbusch started his work (from v. Sengbusch and Zimmermann 1947)

Since the first sweet lupin had been detected, the fact could not be hidden that even though through the sweet genotypes the protein and oil content of the seeds were fully available, and even though this plant species offers many possible uses, starting with soil improvement and ending with the use as a food crop, there has been at least one limiting factor, sometimes more, that impeded breeding progress and therefore lupin growing.

Obviously, there is a relationship concerning yield structure of lupin and its components. This does not mean the differences in yield in favour of the bitter cultivars, which have been reported repeatedly but do vary depending on the environmental conditions of the corresponding locations. As a deficiency mutant the sweet lupin was, from the beginning, at a disadvantage quite naturally. To adjust the yield level of sweet cultivars to that of bitter ones is not a problem any more. But this does mean a relatively low grain yield in proportion to total yield as compared with other crops. On the other hand, considering the steadily growing world population the protein and oil supply derived from grain legumes becomes increasingly a breeding goal of high priority. Also in this connection, the discussion about the utilization of intra- as well as of interspecific variation arose once again. It is worth mentioning that the induction of mutations has been tried but without any convincing results.

Yield in lupin is a complex of interacting components, including earliness of maturity, development of inflorescences on primary stem and successional axillary branches, pod number per inflorescence, seed number per pod, seed size and maturation of pods. Modifications in one of these components will influence total yield. The example of the white lupin demonstrates that under Northwestern European locations a greater yield potential is available from those genotypes that ripen pods on axillary branches than those with ripening pods preferably on main stems. Branching is influenced by the rate of development of primary inflorescences which, on the other hand, are dependent on the requirement for vernalization of the individual genotype and on the degree of apical dominance of primary inflorescence which retards the elongation of successional branches. As far as can be seen from the literature, systematic investigations, which are based on large genetic resources and involve all of these quantitatively inherited characteristics, have not been reported yet. Certainly, yield will strongly be influenced by plant density per unit area and by water supply during the growing season. But these agronomical aspects can be neglected in favour of the breeding point of view.

A special phenomenon, which is common to all grain legumes and most seriously reduces grain yield, is the abscission of pods. Up to now there are no satisfactory interpretations for this. Apparently, imperfect pollination and fertilization do not cause pod abscission, therefore other physiological hypotheses, including hormones, are being discussed. But this is a starting-point which in the case of achieving a successful solution, would result in a substantial increase of yield. This parameter again must not be discussed separately, but in relation to the oil and protein content of seeds. Therefore, the question has to be considered as to what extent yield components are correlated.

As can be expected, the highest correlations to yield are shown by seed and pod number. The last one is easier to handle, moreover it exhibits a sufficient level of heritability. The correlation between pod number and oil content of seeds is positive and sufficiently large, but the amount of genetic determination does not seem to be clear. Less promising is the highly positive correlation between ripening date and oil content. Therefore, a high oil content depends on late ripening genotypes. Last but not least, the high correlation between oil content and time from flowering and pod maturation is of special significance. A long lasting dessication of pods sets up a barrier for adaptation of lupins in northern latitudes.

Taking all correlations into consideration, favourable and unfavourable ones seem to be distributed rather evenly. Selecting genotypes with a measurable thinner pod wall and therefore a shorter period of dessiccation would solve a basic problem in securing grain yields in Northwestern Europe. Since this character has been selected for successfully in other legumes, according to the Vavilovian law of homologous genes it should be possible in lupins as well.

The seed coat could be regarded as another reservoir for selection. In white lupins seed coat provides some 15% of the total seed dry weight, and in the yellow up to 25% compared with only 9% hull of soybeans. Protein content of hulled lupin grains amounts to 20% more than that of unhulled ones. Therefore, thin-coated genotypes would increase protein yield accordingly.

Even though a large intraspecific variation exists which has not been taken advantage of, the possibility of utilizing the interspecific variation is as well being discussed. There are several reasons. So far only 5 of about 300 known species in the genus have been investigated. Moreover, parts of the genus are from the evolutionary point of view in an active dynamic phase. The question is how to make progress by means of interspecific hybrids. A short explanation of the evolution of the genus may be helpful.

Due to the large number of chromosomes in the genus, lupins are considered polyploids. The lack of diploid precursors counts for an old history of evolution. This also is strengthened by the fact that the distribution areas of species are often separated geographically. It can be postulated that the European species, which are analyzed in more detail, very probably are amphidiploids of old origin, functionally behaving as diploids.

Therefore, crossing barriers could be expected and they proved to exist. With the exception of a partial compatibility between *L. luteus* and *L. hispanicus,* the genetic isolation between the South American Andean lupin on one side and the white, yellow and blue lupin on the other seems not to be as strong as had been assumed. Pollen-germination following pollination with the alien species, stimulation of seed development as well as firm pod set, which were observed in some experiments, indicate that the production of interspecific hybrids might be possible. Thus, the objective is to incorporate new characteristics in cross-products to create new combinations – in other words to improve the lupin as a grain legume beyond the phenotypic expression known so far. Already included is *L. cosentinii,* but which is not yet deviating significantly from the known variation. However, North American species of the *L. polyphyllus* type, known as an ornamental plant, would, because of its more balanced proportional relation between vegetative and generative phase, its more uniform and unfailing maturation, add a gene reservoir that without any doubt would broaden the genetic base. Other taxa, preferably of North American origin, could be considered as well. *L. mutabilis,* with its great variation, is also being considered more and more, even in Western Europe, especially here at the place of our festive event, the University of Giessen.

The just mentioned perspectives seem to be attainable more easily by means of unconventional methods in plant breeding than by the classic approach. Therefore, the embryo culture for artificial growing of such

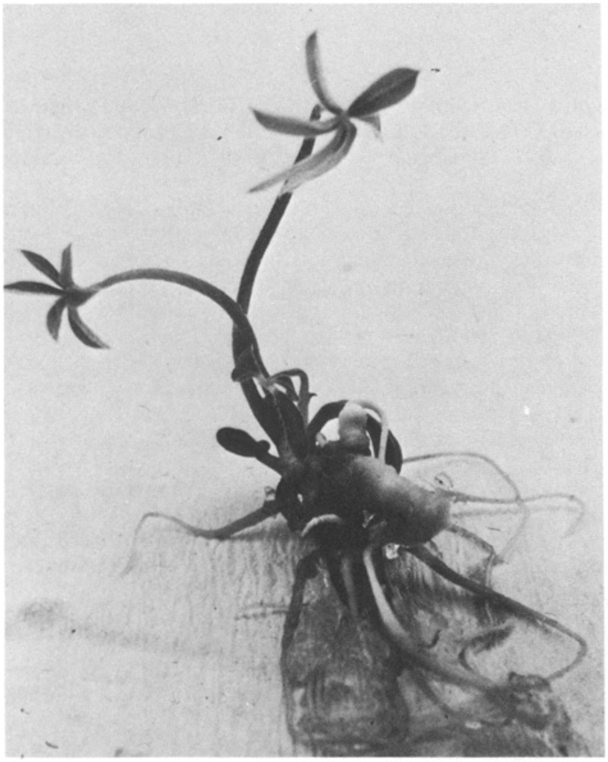

Fig. 6. Plantlet of *L. polyphyllus* from embryo culture

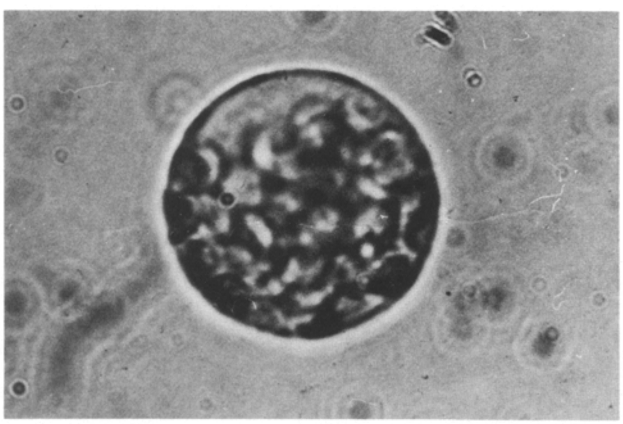

Fig. 7. Isolated protoplast from leaf mesophyll of *L. hartwegii*

crossings, which cannot be developed to full maturity on the plants, the "in vitro"-pollination to produce species hybrids, where the fertilization of the ovule does not operate "in vivo" and the protoplast fusion in order to establish somatic hybrids, should be applied. For these new techniques the lupin is an interesting as well as important research objective.

As an example of the first steps of an unconventional approach the next figures may serve: these show a plantlet grown from embryo culture and an isolated protoplast as implemented by experiments in our institute by Dr. Sator (Figs. 6, 7).

Faced with this encouraging development it should not be forgotten that the lupin is a model for the so-called low input plants, which in connection with economical and ecological problems in agriculture are under discussion, i.e. plants which allow optimizing yield with limited input of means of production. In the extreme case of lupins this stands for minimal tillage before sowing, no plant protection, no irrigation and no application of fertilizers.

The ancient and modern crop plant lupin has passed through an eventful history since it first appeared in Graeco-Roman times and the pre-Columbian civilizations of South America. Nevertheless, it has not come to the end of its evolution. Its present position can be fixed more exactly when the still hidden genetic potentials are revealed.

We have seen the history of a crop plant which perhaps more than other ones allows us to reconstruct our own cultural and social history. On the threshold of its latest evolutionary phase, by which its status of a food crop plant was achieved, great pioneering research had been accomplished by that man in honour of whom we have assembled today, Prof. Dr., Honorary Doctor of Agriculture, Reinhold von Sengbusch.

References

(only summarizing and/or literature compiling publications)

Aguilera JM, A Trier (1978) The revival of the lupin. Food Technol August 1978:70–76

Becker-Dillingen J (1929) Handbuch des Hülsenfruchterbaues und Futterbaues, Band 3. Paul Parey, Berlin

Fruwirth C (1910) Die Züchtung der landwirtschaftlichen Kulturpflanzen. 2. neu bearbeitete Auflage. Paul Parey, Berlin

Gladstones JS (1970) Lupins as crop plants. Field Crop Abstr 23:124–148

Hanelt P (1960) Die Lupinen (Zur Botanik und Geschichte landwirtschaftlich wichtiger Lupinenarten). A Ziemsen, Wittenberg

Mangold HK, Hondelmann W, Pietrzik K, Berger F (1981) Evaluierungshauptbericht Anbau und Verwertung von Lupinen in Peru. GTZ, Eschborn

Schiemann E (1934) Zur Geschichte der Lupine in Deutschland. Züchter 6:33–39

von Sengbusch R (1942) Süßlupinen und Öllupinen (Die Entstehungsgeschichte einiger neuer Kulturpflanzen). Landwirtsch Jahrb 91:719–880

von Sengbusch R (1980) Von der Wildpflanze zur Kulturpflanze (Eine Dokumentation meiner Arbeiten). Selbstverlag, Hamburg

Williams W (1979) Studies on the development of lupins for oil and protein. Euphytica 28:481–488