

Ces arbres seront greffés à nouveau et entreront après contrôle de leur descendance dans le programme d'amélioration du pin laricio, dont les pins dits «de Calabre» introduits en 1823 dans le domaine des Barres par PHILIPPE ANDRÉ DE VILMORIN constituent l'élément principal. Ainsi les idées de deux forestiers précurseurs, sur l'importance des races pour l'un, sur la conservation des caractères héréditaires par le greffage pour l'autre, sont-elles mises à profit, un siècle plus tard, dans le cadre d'une technique fondée précisément sur ces idées, avec pour base de départ les arbres mêmes sur lesquels avaient porté leurs observations.

Résumé

Une vaste expérience de greffage en place de pins laricio de Corse sur pin sylvestre avait été poursuivie à partir de 1820 dans les forêts de la région parisienne et en particulier en forêt de Fontainebleau, en vue de produire en masse des graines de cette essence. Les pins laricio étaient greffés sur place, sur des semis naturels de pins sylvestre, en fente terminale, greffe herbacée. En 1843, plus de 100 000 pins greffés existaient en forêt de Fontainebleau. Il reste encore actuellement une centaine d'arbres dont la plupart ont des dimensions et une forme remarquables.

Summary

Title of the paper: The old Corsican pine grafts of the Forest of Fontainebleau.

A great trial of grafting in situ of Corsican pine on to Scots pine was carried out from 1820 in the forests of the Paris region, and in particular in the forest of Fontainebleau, with the object of mass producing seed of this species. The Corsican pines were grafted in situ, onto natural seedlings of Scots pine, using a terminal cleft graft and succulent scion wood. By 1843 more than 100,000 pine grafts were growing in the forest of Fontainebleau. There still remain one hundred trees, most of which are of remarkable dimensions and form.

Zusammenfassung

Titel der Arbeit: Die alten Zaricio-Kiefer-Pfropfungen im Wald von Fontainebleau.

Ein umfangreicher Freiland-Pfropfversuch mit laricio-Kiefern aus Korsika auf silvestris-Kiefern war seit 1820 in den Wäldern um Paris und besonders im Wald von Fontainebleau zur Durchführung gekommen mit der Absicht, Saatgut dieser Herkunft in großen Mengen zu erzeugen. Die laricio-Kiefern wurden im Freien in Naturverjüngungen der gewöhnlichen Kiefer als krautige Reiser in terminale Spalten der Triebe gepfropft. 1843 existierten im Wald von Fontainebleau mehr als 100 000 Kiefernspfropfungen. Gegenwärtig sind noch 100 Bäume übrig, von denen die meisten beachtliche Dimensionen und eine bemerkenswerte Form haben.

Hardwood Pollen Study

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Introduction

The following short report is a part of a greater study undertaken and in progress at State University College of Forestry at Syracuse University. Its purpose is to fill some of the gaps existing in the knowledge of pollen grain morphology and germination. Tree breeders in the past have placed most of their emphasis upon coniferous pollen investigations, consequently studies of hardwood pollen physiology and particularly hardwood pollen germination are rather scant. The only knowledge which is available on angiosperm pollen is derived from work done on fruit tree pollen.

Literature review

Pollen morphology of gymnosperms and angiosperms was studied as early as the beginning of the 17th century by VON MOHL¹⁾ and in the following decades by investigators such as FRITZSCHE¹⁾. He developed the first pollen classification system which is based upon the various form types of pollen grains. MEYER¹⁾, NÄGELI¹⁾, SCHACHT¹⁾, POLLENDER¹⁾, and FISCHER¹⁾ worked with pollen in the middle of the last century and have provided much information about pollen shape, pollen structure, pollen diameters and pollen physiology. More recent books on the subject were published by WODEHOUSE (1935) and by ERDTMAN (1943, 1947) who give rather detailed information on pollen in general. Investigations on pollen germination and the development

of certain germination techniques, as well as studies of pollen tube growth are of more recent origin. Pollen staining methods have been applied quite frequently to determine viability. It is felt however, that they are not necessarily an adequate substitute for actual germination tests. Germination techniques and pollen tube growth for *Pinus strobus* L. and *Pinus resinosa* Ait. have been investigated by DUFFIELD and SNOW (1941) and that of *Pinus ponderosa* LAWS. by RIGHTER (1939).

Previous workers have used a wide variety of media for artificial germination of pollen. They also have shown that certain tree species have specific requirements with regards to storage conditions, oxygen, light, temperature, humidity, and other environmental conditions during the process of germination.

Three main methods are widely used in germinating pollen. They are (a) the hanging drop method described by RIGHTER (1939) (b) the agar gel method described by DUFFIELD and SNOW (1941) and (c) the vapor method described by VON WALDERDORFF (1924) and used also by DUFFIELD in a modified form.

VAN TIEGHAM as early as 1869²⁾ demonstrated the necessity of oxygen for pollen germination. He sowed pollen in a drop of water, placed a cover glass over it, and noted that only the grains at the periphery emitted tubes. When the cover glass was lifted the remainder grew. VAN TIEGHAM

¹⁾ See WODEHOUSE, 1935.

²⁾ See ERDTMAN, 1952.

also secured evidence that during the elongation of the pollen tube oxygen was removed from the surrounding air and replaced by carbon dioxide. MANJIN (1886)³⁾ reported that in artificial cultures the respiratory ratio gradually falls from the time of germination until the cell dies.

Ideal temperature and humidity conditions among tree species for germination differ as they do for storage BRINK (1924) and JOHNSON (1943). The best all around temperature for pollen germination was found to be 25° C (77° F), and was used by most workers. The humidity maintained by JOHNSON (1943) in the germination chambers approached saturation. DUFFIELD (1954) disagrees with the high humidity used by JOHNSON, but explains that JOHNSON used different germination methods, and attributes the difference to contrarities in storage humidities.

The effect of light and darkness on pollen germination and pollen tube growth was studied by BRINK (1924) and JOHNSON (1943). Both workers found that there was no significant difference in germination data after incubation under light or dark conditions. JOHNSON (1943) however, found a significant increase in the germ tube length in samples incubated in light. This may be taken to indicate that after germination has taken place, light has a slight stimulatory effect on the rate of pollen tube growth.

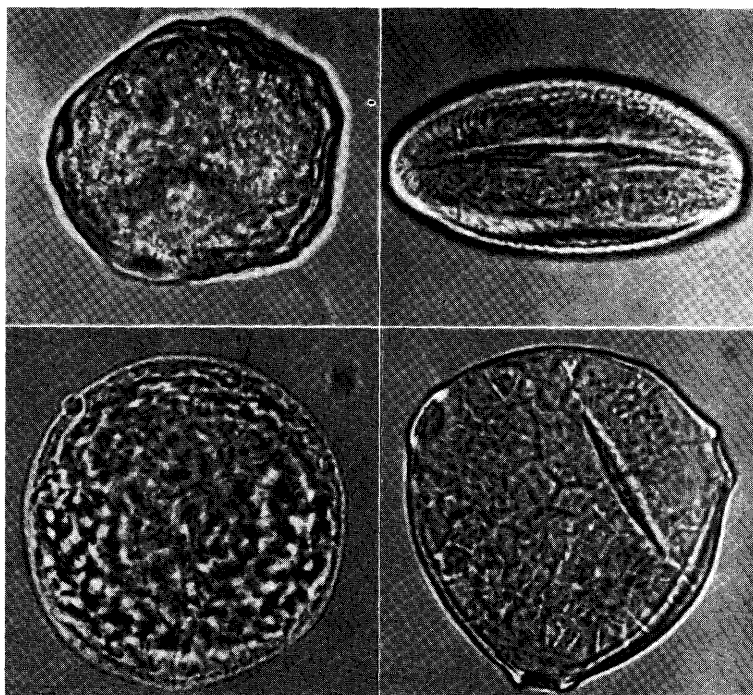
Pollen grains, like seeds, are provided with a considerable amount of food material in the form of carbohydrates or fats. These foods are mostly sufficient for initial pollen tube growth, but outside sources of nutritive material are necessary to keep the tube growing (BRINK [1924], KIRKWOOD [1906], DUFFIELD [1954]). DALMER (1880) revealed that reserve food materials are freely distributed in the tissues leading to the ovules. These reserves are present in the form of readily diffusible sugars..

In experiments with fruit tree pollen collected from the same tree and the same branch but different flowers; KOBEL (1954) found a considerable variation of pollen germination. Highest germination was obtained from pollen induced by flowers close to the main food source, i. e. stem. It is also most likely that the amount of stored food in the grains will differ in the same tree from year to year.

Material

Four hardwood tree species widely distributed in New York State, were chosen for our experiment. The species were: *Ulmus americana* L., *Prunus serotina* EHRH., *Populus tremuloides* MICHX., and *Betula papyrifera* MARSH. For each species pollen of only one tree was included in our investigation. The pollen of *Populus tremuloides*, *Betula papyrifera* and *Ulmus americana* were collected at the beginning of March from branches kept in ice water in the greenhouse. The pollen of *Prunus serotina* was collected at about the same time from healthy grafts in the greenhouse.

At the time of flowering the pollen was gathered by gently tapping the flowers and catching the fallen pollen on a sheet of paper. Any foreign material mixed in with the pollen was eliminated by a mild motion of the sheet of paper which separated the pollen grains from other material. The pollen was then put into open glass vials,



Figs. 1—4. — Photomicrographs of pollen (from left to right). — 1. *Ulmus americana* (ca. $\times 2250$). — 2. *Prunus serotina* (ca. $\times 2950$). — 3. *Populus tremuloides* (ca. $\times 2250$). — 4. *Betula papyrifera* (ca. $\times 2025$).

placed in a desiccator with calcium chloride, and refrigerated at 10° C until use (approximately two weeks later).

Pollen morphology

The morphology of the pollen under study was examined using a Bausch and Lomb research microscope and photomicrographs were taken through the same microscope with a Bausch and Lomb L series camera adapted to this type of photography. All photomicrographs are oil immersion photos. The mounting medium for embedding the pollen was also immersion oil, used in hopes of getting better resolving power, thus enabling us to see more detail. Photographs of the pollen tubes were taken, using the same equipment.

To obtain the diameter range of the pollen under consideration 25 measurements were made for each species and the results averaged. The pollen grains as well as the tube lengths were measured in microns by means of a calibrated eyepiece and a stage micrometer.

Ulmus americana (Figure 1): The pollen grains of this species average about 32 microns in diameter and the number of germ pores was most commonly 5, occasionally 7, arranged around the equator. Polar views suggest a pentagon in outline, while the sculpturing of the exine is reticulate suggesting the surface markings of a peanut shell. The sculptured pattern may also be due to impressions in the adhesive substances on the exine of the species. (There is a certain similarity to pollen of *Betula papyrifera*. Arci⁴⁾ or arcoid streaks are present in both species.)

Prunus serotina (Figure 2): The normal grains of this species are tricolpate, with rather long furrows tapering to pointed ends. The grains are ellipsoidal when dry, as shown in Figure 2, but become oblately flattened and angular upon taking up moisture. In size they are about 25 microns in diameter. The exine is more or less granular in appearance

⁴⁾ Arci — band like, locally thickened parts of the exine, extending in sweeping curves from aperture to aperture.

³⁾ See BRINK, 1924.

with the granules arranged in rows, looking somewhat striate.

Populus tremuloides (Figure 3): The diameter of the pollen of this species averages about 30 microns, and it is spheroidal or a bit irregular in shape. The grains have no germinal furrows and the exine is granular in appearance. Intine is thick; not so the exine.

Betula papyrifera (Figure 4): The grains average about 30 microns in diameter and are angular in appearance when seen in the polar view. Three germinal furrows are usually present (sometimes 2 or 4). The pollen is circular in shape and the exine is granular.

Germination medium

Upon experimenting with the germination of hardwood pollen, using the hanging drop method as described by RIGHTER (1939), it was found that the pollen gave a very low germination per cent and tended frequently to burst. An agar medium with 10% sucrose; however, gave satisfactory results and was also very suitable for observing the course of growth of the pollen tubes. The agar medium consists of the following ingredients: 500 ccm of distilled water, 20 grams of agar and 50 grams of sucrose. The solution was autoclaved for 20 minutes at 15 pounds pressure. The petri dishes into which the agar was poured were first wrapped in a paper toweling and put into the oven for one hour at 160° C. The table onto which the sterilized dishes were to be set was decontaminated with Purex³⁾. While the agar solution was still hot, about 5 minutes after coming out of the autoclave, it was poured into the petri dishes. The covers of the dishes were opened only wide enough to facilitate pouring, thus decreasing the chance for any spores to enter the dish. The agar was poured about 1/8 of an inch (about 3 mm) thick in the dish, and the dishes were then stored in the refrigerator until used.

Germinating the pollen

A small quantity of pollen was blown across the surface of the agar media, and a few drops of distilled water were used to wet the inside of the petri dish cover. The last step insures that a relatively high humidity will exist in the dish. The cover was then placed on the dish and the dish kept under normal light at 25° C (77° F). The time of germination was noted along with the speed of growth of the pollen tube for each species.

Experimental results

More than 65% of the pollen of *Prunus serotina* began to germinate within 40 minutes after being placed upon the agar media and about 60% of the pollen of *Populus tremuloides* germinated within 70 minutes, while only 1% of the *Betula papyrifera* pollen had begun to germinate after 75 minutes. *Ulmus americana* did not germinate. The growth of the pollen tubes was measured every hour after germination until growth was negligible.

³⁾ Purex — Sodium chloride solution for sterilization.

Figure 5 shows three pollen tubes of *Prunus serotina* of which two are normally developed but one burst at the end of its course of growth. The specific reason for this bursting cannot be given.

Figure 6 illustrates a pollen tube of *Populus tremuloides* approximately four hours after germination.

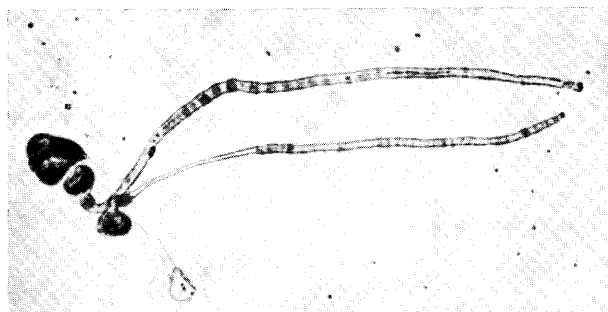


Fig. 6. — Photomicrograph of germinating *Populus tremuloides* pollen (ca. $\times 120$).

Figure 7 shows two pollen tubes of *Betula papyrifera* also four hours after germination. The length of the pollen tubes is rather short in comparison with the former species.

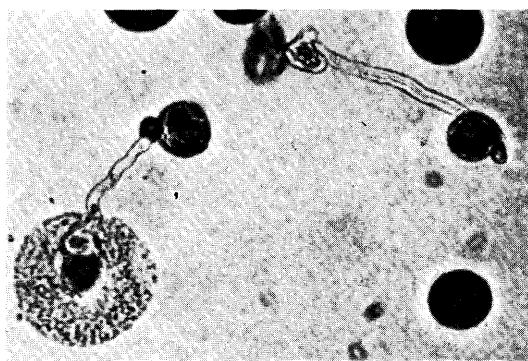


Fig. 7. — Photomicrograph of germinating *Betula papyrifera* pollen (ca. $\times 260$).

Figure 8 represents the growth curves of the pollen tubes of the above mentioned tree species. The curves were obtained by measuring 10 pollen tubes of each species selected at random.

Observations during the elongation of the various pollen tubes, and study of the growth curves, provide the following general information:

1. The greatest growth of the pollen tubes for each species occurred in the first three hours, slowing down considerably until it reached a length where no visible elongation could be observed. This point was normally reached after 7 or 8 hours.
2. The pollen tubes of *Populus tremuloides* were the longest, averaging about 750 microns. Next in order was *Prunus serotina* which extended its pollen tubes to an average length of about 510 microns. The shortest pollen

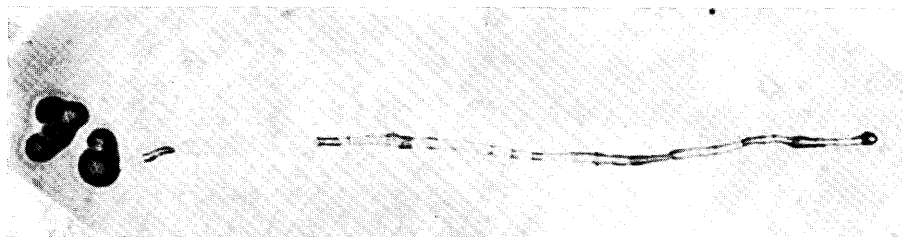


Fig. 5. — Photomicrograph of germinating *Prunus serotina* pollen (ca. $\times 140$).

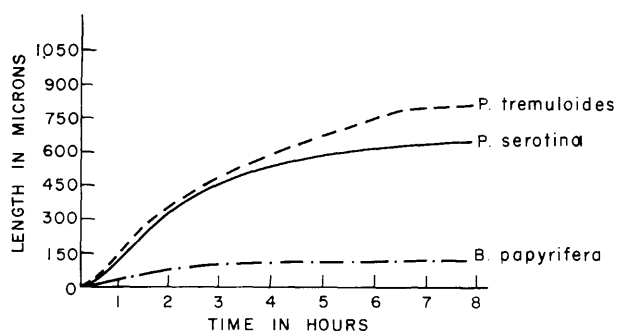


Fig. 8. — Growth curves of pollen tubes of *Populus tremuloides*, *Prunus serotina*, and *Betula papyrifera*. The curves are based on 10 pollen tubes for each species selected at random.

tubes were observed in *Betula papyrifera*, averaging only about 120 microns. The diameters of the pollen measured in order are: 30 microns, 25 microns, 30 microns.

3. No significant relation was found between the length of tube and delay in initiation of germination. All either germinated 40 — 75 minutes or very shortly after being placed onto the medium or they did not germinate.

4. There seems to be a positive correlation between the number of pollen which germinated and pollen tube growth in the sense that the higher the germination % the longer the pollen tubes. (*Populus tremuloides* and *Prunus serotina* germinated 60% or 65% respectively, while *Betula papyrifera* germinated approximately 1% only).

5. Bursting of pollen tubes occurred very seldom and was found only in *Betula papyrifera* and *Prunus serotina*.

Discussion

The differences in total germination between the four tree species were greater than expected. This variation may be due to storage conditions, humidity and temperature during storage; or germination technique. DUFFIELD, SNOW (1941) and JOHNSON (1943) have found that the pollen of some conifers is very sensitive to the fore-mentioned factors. This could also be the case with hardwood pollen, in the sense that the storage and germination conditions may have been more favorable toward *P. tremuloides* and *Prunus serotina*, while less so for the other two species. Another possibility is that calcium chloride is too severe a desiccating agent in the storage of some hardwood pollen resulting in an excess loss of moisture of the pollen.

There is however, still another possibility for low germination of *Betula papyrifera* and no germination of *Ulmus americana*. KOBEL (1954), and others, have found a significant variation in germination in certain fruit trees depending on the location of the flowers. The branch from which the *Betula papyrifera* pollen was obtained was from the lowest crown section and the male catkin was located on its far outside end. In the case of *Ulmus americana* the branch was obtained from a tree approximately 70 years old which was quite heavily attacked by Dutch elm disease. Pollen from the same branch used in intraspecific greenhouse hybridization experiments did not result in any viable seed while pollen from other trees of the same species was quite effective. We might assume therefore, that the lack of enough food or low pollen quality resulted in very little or no germination. (A later experiment with another *Ulmus americana* pollen source stored for almost 6 months under conditions mentioned above resulted in approximately 30 per cent germination. Pollen tube growth however, was not measured)

DUFFIELD's statement that germination per cent and pollen tube growth are highly and positively correlated was demonstrated by our study.

The bursting of pollen tubes shortly after germination or after a certain pollen tube elongation is believed to be influenced by a number of factors not yet understood or controlled by our present techniques. Some workers believe it to be merely an osmotic phenomenon. DUFFIELD (1954) suggests that a wide variety of conditions of pollen storage, humidity and germination techniques are responsible. Actually very little bursting was noticed in this experiment, i. e. in the germination medium described above.

Conclusion

The principle conclusions which can be drawn from this short study is that much more knowledge and experimentation is needed as regards the storage and germination of angiosperm pollen. The methods of extraction, storage and germination as described in this report appear to be satisfactory for practical use with *Prunus serotina* and also for *Populus tremuloides* pollen which loses its viability very quickly. At the same time one or more of these factors might be unsatisfactory for *Betula papyrifera*. Future experimental work will help to answer a number of questions and problems not satisfactorily solved by this study.

Summary

A small study was initiated to test well known pollen germination techniques using pollen of *Ulmus americana*, *Prunus serotina*, *Populus tremuloides* and *Betula papyrifera*. An agar medium with 10% sucrose was found most satisfactory for pollen of *Prunus serotina* and *Populus tremuloides*. Two other hardwood species; *Betula papyrifera* and *Ulmus americana*, did poorly in our experiments. It is felt, however, that causes other than storage and germination conditions are mainly responsible for our results. The speed of germination as well as pollen tube length has been measured indicating that there is a positive correlation between germination per cent and pollen tube length. More experimental work is needed and will be undertaken with hardwood pollen.

Zusammenfassung

Titel der Arbeit: Untersuchung mit Laubholzpollen.

Allgemein bekannte Methoden für Pollenkeimung wurden hinsichtlich ihrer Brauchbarkeit für *Ulmus americana*, *Prunus serotina*, *Populus tremuloides* und *Betula papyrifera* untersucht. Agar Media mit 10% Sucrose ergaben sehr günstige Resultate für *Prunus serotina* und *Populus tremuloides*. Die beiden anderen Laubholz-Arten reagierten mehr oder weniger negativ. Es wird jedoch angenommen, daß andere als Aufbewahrungs- und Keimbedingungen dafür verantwortlich gemacht werden müssen. Messungen der Keimgeschwindigkeit und der Länge der Pollenschläuche lassen den Schluß zu, daß eine positive Korrelation zwischen Keimprozent und der Länge der Pollenschläuche besteht. Zusätzliche Untersuchungen mit Laubholzpollen sind notwendig und sollen unternommen werden.

Résumé

Titre de l'article: Etude sur le pollen des feuillus.

Dans une petite étude, les auteurs ont essayé les techniques classiques de germination du pollen avec les espèces suivantes: *Ulmus americana*, *Prunus serotina*, *Populus tremuloides* et *Betula papyrifera*. Le meilleur milieu pour le pollen de *Prunus serotina* et *Populus tremuloides* est un

milieu gélosé avec 10% de saccharose. Les deux autres feuillus: *Betula papyrifera* et *Ulmus americana* donnèrent des résultats médiocres dans ces expériences. Il est probable que des causes autres que les conditions de conservation et de germination en sont surtout responsables. La vitesse de germination et la longueur du tube pollinique ont été mesurées et une corrélation positive décelée entre ces deux facteurs. De nouvelles études sont nécessaires et vont être entreprises.

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Keimschnelligkeit als Erbeigenschaft

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Unter Keimschnelligkeit — früher auch Keimenergie genannt — versteht man den Prozentsatz keimfähiger Samen, der in einem bestimmten verkürzten Abschnitt des gesamten Keimzeitraumes keimt. Der Zeitraum zur Bestimmung der Keimfähigkeit und der verkürzte Zeitabschnitt zur Ermittlung der Keimschnelligkeit sind nach Baumart verschieden; ihre Zeitdauer ist für die amtliche Samenprüfung im sog. landwirtschaftlichen Methodenbuch (EGGEBRECHT 1949) verbindlich festgelegt. Bei Fichte zum Beispiel beträgt die Zeitspanne zur Feststellung der Keimschnelligkeit 7 Tage, bei Kiefer nur 4 Tage. Während die Frage der Keimschnelligkeit bisher hauptsächlich im Zusammenhang mit der Pflanzenausbeute, also mit dem Pflanzenprozent eine Rolle spielte, wurde sie erneut aktuell im Zusammenhang mit Fragen der forstlichen Genetik und Züchtung (BARTELS 1953, SCHRÖCK und STERN 1953, E. und M. ROHMEDE 1955).

Auf die Einmaligkeit der Erscheinung der Lebewesen Waldbäume haben besonders KÖSTLER (1950) und ROHMEDE (1953) hingewiesen. Die mehr oder minder deutlich wahrnehmbaren Unterschiede von einem zum anderen Einzelbewesen auch innerhalb der kleinsten Einheit unseres botanischen Systems, nämlich der Varietät oder Sorte, sind durch den Erbanlagenbestand bestimmt. Das durch den Erbanlagenbestand in seinem Grundtyp bestimmte Erscheinungsbild wird jedoch stark durch die Umweltbedingungen variiert. Ebenso wie die einzelnen Pflanzen sind auch die einzelnen Samen einer Saatgutpartie niemals von gleichem Wert. Sie unterscheiden sich, wenn man sie zum Beispiel in entsprechend großer Vergrößerung betrachtet, in morphologischen Eigenschaften, z. B. Länge, Breite, Form, Wölbung, Farbe usw. und außerdem in ähnlicher Weise in ihrem keimungsphysiologischen Verhalten. Diese Unterschiede können ihre Ursache in der verschiedenen genetischen Ausrüstung der Samen haben, liegen aber meist in scheinbaren Zufälligkeiten begründet, die in ihrer Gesamtheit von GERM (1953) im Unterschied zur genetischen Ausrüstung als somatische Ausrüstung bezeichnet werden. Eigene Untersuchungen über

die Faktorenabhängigkeit der Keimschnelligkeit haben gezeigt, daß die Keimschnelligkeit weit mehr als die Keimkraft durch topo-, cyclo- und perigene Einflüsse bestimmt wird. Hinzu kommen die vielfältigen Wirkungen der Umweltfaktoren während der eigentlichen Keimung, d. h. vom Zeitpunkt des Einquellens ab. Im Ganzen wird die Keimschnelligkeit so sehr durch Faktoren der Umwelt bestimmt, daß diese in ihrer starken Wirkung eine erblich bedingte, von den Durchschnittswerten abweichende Keimschnelligkeit oder Keimverzögerung wohl in den meisten Fällen verdecken werden. Dies und die Schwierigkeit, die Einflüsse der einzelnen Faktoren klar abzugrenzen, sind wohl die Gründe, daß nur wenige Arbeiten bekannt sind, deren Ergebnisse darauf hinweisen, daß die Keimschnelligkeit als Individualeigenschaft und damit als kennzeichnendes Merkmal für die Verschiedenheit in der Erbanlage innerhalb einer Art angesprochen werden kann.

Es interessiert vor allem die Frage, ob eine keimungsphysiologische Eigenschaft wie die Keimschnelligkeit als charakteristisch für eine Populations- oder Individualnachkommenschaft gelten kann und sich als signifikantes und auf die weitere Leistung des Sämlings über das Stadium der Keimung hinaus etwas aussagendes Merkmal bei Frühtesten zur Nachkommenschaftsprüfung verwenden läßt. Die Eignung der Keimschnelligkeit als Testfaktor wird von einigen Autoren z. B. für Provenienz-Diagnose bejaht (KARSCHON 1949 und HAASIS und THRUPP 1931) und für Wuchskraftprognosen zunächst in Frage gestellt (SCHRÖCK 1951, SCHRÖCK und STERN 1953).

1888 beschreiben NOBBE und Mitarbeiter in der Arbeit „Über den Einfluß der Keimungsenergie der Samen auf die Entwicklung der Pflanzen“, daß man an Levkojen bei allen beobachteten Sorten feststellen konnte, daß u. a. die schnellkeimenden überwiegend gefüllte, die träge keimenden Samen ebenso überwiegend einfache Blumen lieferten. Daß die Anlage zu schneller Keimung in diesem Fall erblich bedingt ist, erhielten die Verfasser durch nachfolgend durchgeführte Kreuzungsversuche bestätigt. Arbeiten von KAPPERT (1957) haben später gezeigt, daß gefüllte Levko-