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Activation of Teliospore Germination in *Uromyces appendiculatus* var. *appendiculatus*[1])

I. Aging and Temperature

By

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With 8 figures

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Abstract

The effects of aging and temperature on teliospore germination in *Uromyces appendiculatus* var. *appendiculatus* were studied.

1. Indoor storage was good at ~ 4 °C in the dark. Under these conditions spores remained dormant for ~ 9 mo, but thereafter germination gradually increased to a maximum (~ 63 %) after 36 mo. Spores stored outdoors showed a marked increase in germination after ~ 4 mo and reached maximum (~ 73 %) at 7—8 mo.

2. The optimum temperature for germination was at 18 °C. While freezing (—18 °C) and thawing (20 °C) had no beneficial effect on spore germination, heat treatments from 30—32 °C for 3—4 d proved effective in activating teliospore germination. Heat treatments caused an increase in spore mortality. Basidiospore release from heat-treated teliospores was markedly reduced compared to control spores.

3. In all experiments the emergence of metabasidia was preceded by an obligatory 3—5 d lag period regardless of the treatment given, the age or level of germinability of treated and control spores.

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[1]) This study represents a portion of a dissertation submitted by the senior author to the Faculty of Biology of the University of Konstanz in March, 1983, in partial fulfillment of the requirements for the degree of Doctor of Natural Sciences (Dr. rer. nat.).

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Zusammenfassung

Die Aktivierung der Teleutosporenkeimung bei *Uromyces appendiculatus* var. *appendiculatus* durch Lagerung und Wärmebehandlung

Es wurde der Einfluß von Sporenlagerung und Temperatur auf die Teleutosporenkeimung bei *Uromyces appendiculatus* var. *appendiculatus* untersucht.

1. Gute Lagerungsbedingungen für die Sporen waren bei 4 °C im Dunkeln gegeben (Beobachtungszeitraum 4 Jahre). Hierbei blieben die Sporen ~ 9 Monate im Ruhestadium, danach stieg ihre Keimfähigkeit allmählich auf ein Maximum (~ 63 %) nach 36 Monaten an. Im Gegensatz dazu waren Sporen, die auf dem Feld überwinterten, schon nach 4 Monaten keimfähig und erreichten ihr Maximum (~ 73 %) nach 7—8 Monaten.

2. Das Temperaturoptimum der Teleutosporenkeimung lag bei 18 °C. Der Einfluß von Kälte- und Wärmebehandlungen auf die Sporenkeimung wurde eingehend untersucht. Obwohl mehrmaliges Einfrieren und Auftauen keine wesentliche Aktivierung der Keimung ergab, waren Wärmebehandlungen bei 30—32 °C für 3—4 d sehr wirksam. Eine geringe Erhöhung der Mortalitätsrate und eine starke Beeinträchtigung der Abschleuderung von Basidiosporen waren weitere Folgen der Wärmebehandlung.

3. In allen Versuchen, unabhängig von der gegebenen Behandlung, dem Alter oder der Keimfähigkeit der Teleutosporen, wurde beobachtet, daß nach einer obligatorischen Lagphase von 3—5 d das Metabasidium die Keimpore durchbrach und sich dann voll ausbildete.

The teliospores of many agriculturally important rusts (e. g. *Melampsora lini, Puccinia graminis, Uromyces appendiculatus* var. *appendiculatus*) remain dormant for several months after formation. Problems associated with activating such spores to germinate readily have hindered studies of taxonomy, pathogenicity, and microscopy of the initial stages of basidiospore penetration and infection (see MENDGEN 1983). Many studies on teliospore germination have been conducted, but very few provide quantitative and/or qualitative information for species possessing dormant teliospores (BINDER *et al.* 1977, BLANK and LEATHERS 1963, HORNER 1963, KLISIEWICZ 1977, NEUHAUS 1969). Various methods of stimulating germination of dormant teliospores have been reported, including: cool laboratory storage, natural weathering, wetting and drying and/or freezing and thawing (see GOLD and STATLER 1983, MENDGEN 1983), chemical treatment (BINDER *et al.* 1977), application of host substances (KLISIEWICZ 1972, 1973), prolonged incubation on agar or water (GROTH and MOGEN 1978), and control of light (NEUHAUS 1969). Unfortunately, the reproducibility of these methods with similar isolates and their applicability to other rust species is unsatisfactory or unknown.

Teliospores of *Uromyces appendiculatus* var. *appendiculatus*[3]) (bean rust) were chosen for the present study. In the first part of this study, the effects of aging and temperature on the activation and pattern of teliospore germination were studied quantitatively and qualitatively.

Preliminary reports of this research have been published earlier (GOLD and MENDGEN 1981 a, b).

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[3]) Synonyms: *Uromyces phaseoli* (Pers.) Wint. and *Uromyces phaseoli* (Pers.) Wint. var. *typica* Arth. See BOEREMA and VERHOEVEN (1979) and CUMMINS (1978) for an accurate nomenclatural account of these and related species.

Material and Methods

1. Fungal isolates

The bean rust isolates are listed in direct relation to the extent in which they were experimentally studied:

Fungus	Origin	Symbol
U. appendiculatus var. *appendiculatus*	Lahr Valley, Black Forest, W. Germany	SWBR
U. appendiculatus var. *appendiculatus*	Göttingen, W. Germany	GBR
U. appendiculatus var. *appendiculatus*	Reichenau Island, Lake Constance	RBR 1
U. appendiculatus var. *appendiculatus*	Constance, W. Germany	KBR 1

The following isolates were only briefly studied for comparison:

Phragmidium mucronatum	Kerry County, Ireland
Phragmidium violaceum	Mainau Island, Lake Constance, W. Germany
Puccinia carthami (1)	Davis, California, USA
Puccinia sorghi (2)	Zürich, Switzerland
Uromyces dianthi (3)	Littlehampton, England
Uromyces scuttelatus	Constance, W. Germany

The original uredinial or telial culture was kindly provided by:

1. Dr. J. M. Klisiewicz, University of California-Davis.
2. Mr. T. Ullman, Eidgenössische Technische Hochschule, Zürich.
3. Dr. D. M. Spencer, Glasshouse Crops Research Institute, Littlehampton.

2. General

The fungus, *Uromyces appendiculatus* var. *appendiculatus*, was increased for all experiments on susceptible garden bean (*Phaseolus vulgaris* L., cv. Favorit). The plants were grown in a growth chamber held at 18 ± 0.5 °C, ~ 70 % RH under 10 000 lx (16 h photoperiod). Fourteen day old primary leaves were inoculated with an urediniospore suspension (~ 30 mg/100 ml distilled water with 0.05 % Tween 20) and incubated under dim light or in the dark at 18—20 °C and 100 % RH for 20—24 h. Secondary growth of the bean plants was removed biweekly. At 7—10 d after inoculation, uredinia were present on both ad- and abaxial leaf surfaces and heavy sporulation began. From 2—3 wk after initial sporulation, teliospore production gradually replaced urediniospore formation in uredinia accompanied by teliospore production in separately developing telial sori. Mature teliospores were collected 2—3 times weekly by gently brushing the infected leaves over aluminium foil. Teliospores were stored in closed glass vials in a refrigerator held at ~ 4 °C and ~ 70 % RH in the dark.

For the germination experiments teliospores were evenly brushed onto a hydrophilic cellulose nitrate filter (Sartorius, 8 μm pores) on purified 2 % glass-distilled water agar (Merck) in 6 or 9 cm plastic Petri dishes (Greiner). The rapidly evaporating fluorochemical liquid FC-75 (3M Brand Inert Fluorchemical Liquid) was used as carrier for the spores. The evenly spread spore mass (~ 200 teliospores/mm^2) appeared as a light brown monolayer. The plates were kept at 18 ± 0.5 °C under 1000 lx (16 h photoperiod = 06.00—22.00 h, light; 22.00—06.00 h, dark).

3. Sampling and statistical analysis

In all experiments, 200—300 spores were tallied in each of 3—5 replicates for each treatment per examination date. Each experiment was repeated a minimum of 2—3 times. Observations were made at ×500 or ×640 using a Zeiss Universal microscope equipped with interference-contrast optics. Spore samples were scored for germination, mortality, and in some cases for vacuolation. Spores were considered to be germinated when the metabasidium or portions therefrom were distinguishable beyond the limits of the apical germination pore and dead when the cytoplasm appeared anucleate and disorganized. All values represent total percentage germination, mortality, or vacuolation, respectively.

The results were analysed using Wilcoxon's rank test (Figs. 2, 4, 7, 8b) or Chi-square (χ^2) from fourfold tables (Figs. 5, 8). Statistical differences with a significance level of $P < 0.05$ are indicated with an star (*).

4. Influence of aging on teliospore germination

Teliospores of SWBR were produced in the fall and winter of 1978 in growth chambers and stored at 4 °C as described above. As comparison, naturally overwintered spores of RBR 1 from field grown pole beans (1981) were tested. In this experiment, 2 alternate methods of overwintering were employed. In the first case telia-laden trifoliate leaves were collected randomly from the plants and air dried for 7 d in a cool greenhouse. The dried leaves were placed into a jute sack that was hung on the outside of a shed. The sack was not in direct sunlight and was protected from rain- and snowfall. The second alternative was simply to leave the infected pole beans standing with no protection or special precautions to minimize natural weathering. For all germination tests, spores were scored for percentage germination and mortality after 15 d incubation on 2 % water agar at 18 °C under 1000 lx (16 h/d). During the field experiment weather data was recorded daily from October 1, 1981 to May 1, 1982 with a hygrothermograph housed in a small weather station ~ 20 m away from the field plot.

5. Influence of temperature on teliospore germination

5.1. Temperature optimum

The optimum temperature for teliospore germination was investigated with naturally overwintered spores of RBR 1 from above. Spores, which had been stored in the jute sack for 8.5 mo, were incubated on 2 % water agar at either 4, 8, 12, 16, 18, 20, 23, 26 ± 0.5 °C under 1000 lx (16 h/d) for 15 d. Percentage germination and mortality were calculated at 15 d.

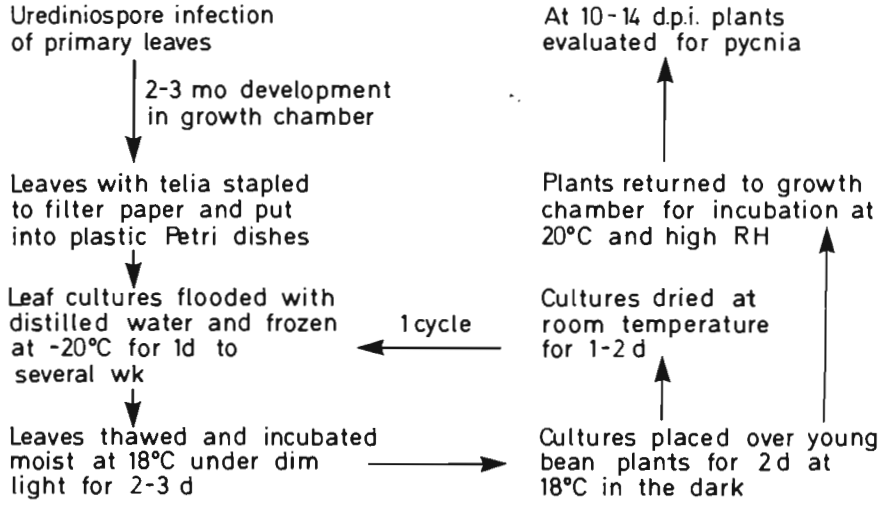


Fig. 1. Freeze-thaw and wet-dry cycling scheme for telia on primary bean leaves

5.2. Cold treatment

Telia-laden primary bean leaves were exposed to as many as 15 alternate periods of freeze-thaw and wet-dry conditions and periodically tested for teliospore germination as described in Fig. 1.

5.3. Heat treatment

Teliospores were spread onto agar as described above and heat treated *in situ*. In preliminary experiments spores of SWBR were subjected to temperatures of 28, 30, 32, or 34 ±1.0 °C for 4 d in incubation chambers without light. For comparison spores of GBR were treated at 32 °C for 4 d. Following the heat treatments spores were then incubated with the untreated controls at 21 ± 1.0 °C. Microscopical evaluations were made regularly for several weeks after each respective treatment and for the controls. The spores were only exposed to light during handling or microscopical evaluations.

Subsequent heat treatments were performed in complete darkness at 31.6 or 32.0 ± 0.1 °C. Thereafter, the treated and untreated control spores were incubated at 18 ± 0.5 °C under 1000 lx (16 h/d). The Petri dishes were not sealed air-tight to avoid flooding of the agar surface and to prevent water condensation and drop formation inside the plates.

Two main experiments were conducted: (1) SWBR spores were treated at 31.6 °C for 1, 2, 3, or 4 d and then incubated together with the untreated controls at 18 °C. Percentage germination, mortality, and vacuolation were determined up to 15 d after each respective treatment. (2) Fresh versus refrigerator-stored spores of SWBR and GBR were treated at 31.6 °C for 3 d and then evaluated for percentage germination under normal laboratory conditions.

Results

1. Influence of aging on teliospore germination

The effect of long term storage at 4 °C in the dark on teliospore germination and mortality is summarized in Figure 2. Teliospores remained dormant for ~ 9 mo, but thereafter a gradual increase in their germinability occurred. At 16 and 24 mo for germination and mortality, respectively, a significant increase over fresh teliospores was observed. Between 24 and 36 mo

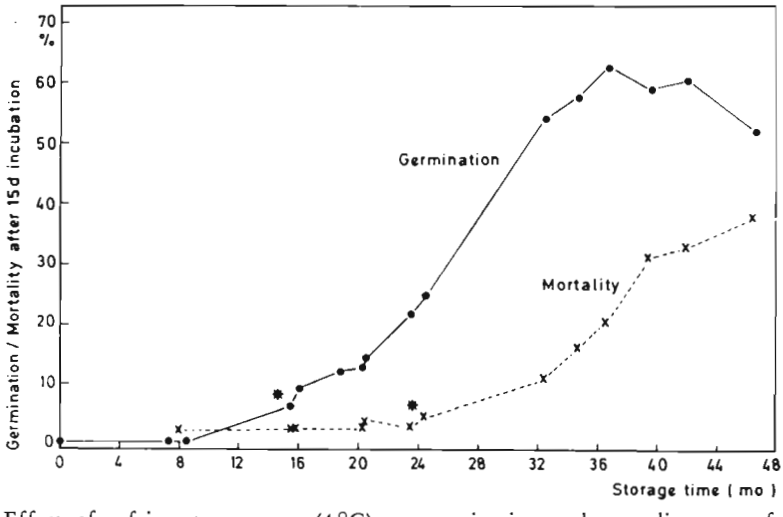


Fig. 2. Effect of refrigerator storage (4 °C) on germination and mortality rate of SWBR teliospores. All means after 16 mo for germination and 24 mo for mortality are significantly larger than controls ($P < 0.05$)

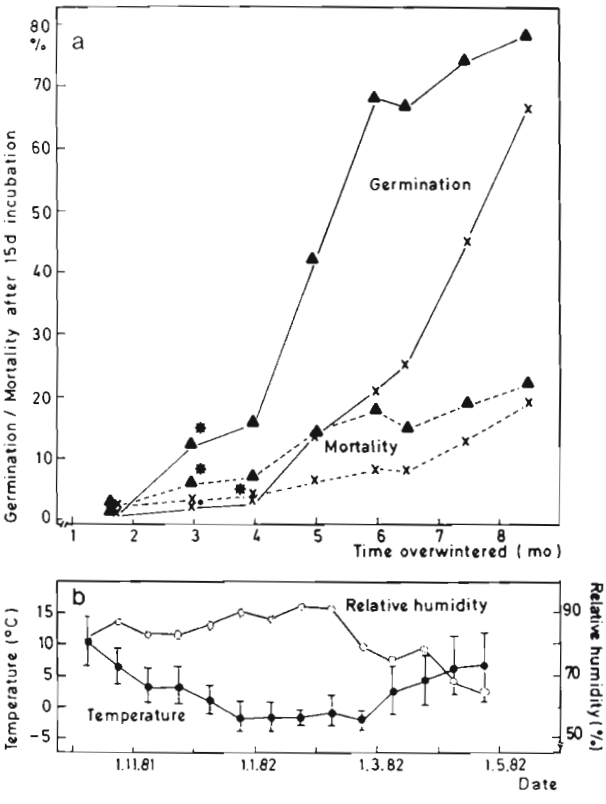


Fig. 3. (a) Effect of outdoor storage on germination and mortality rate of RBR 1 teliospores. Spore-laden leaves were stored either dry in a jute sack (x) or left hanging on bean plants in the field (▲); (b) Weather information: mean temperature (●) with average maxima and minima; mean percent relative humidity (o). All points are based on 12 bihourly readings/d averaged over 15 d (= bimonthly averages)

the level of germination reached its maximum and declined thereafter due to the constantly rising level of mortality. The effects of outdoor storage on teliospores of RBR are shown in Figure 3. Spores were stored either protected from rain and snow under generally dry conditions (= dry) or exposed to weather under generally moist-wet conditions (= wet). In both populations a significant increase in germination and mortality over the control values (= start values) was found after a 3—4 mo outdoor exposure. Thereafter, an extremely rapid increase in germination and a steady rise in mortality developed in both the dry and wet treated populations. Although the increase in germinability of the wet spores arose much earlier and was more pronounced than in the dry spores, the 2 groups showed a converging trend of development between 6 and 8.5 mo. After one year storage outdoors ~ 99 % of the dry spores were dead; wet spores were no longer available for examination.

2. Influence of temperature on teliospore germination

2.1. Temperature optimum

Germination occurred within 3—5 d for spores incubated between 12 and 23 °C. The rate of germination was highest between 16 and 20 °C; no germination occurred at 4 or 26 °C (Fig. 4). After 15 d incubation the ger-

mination optimum was observed at 18 °C ($P < 0.05$). The rate of spore mortality gradually increased from 14 to 32 % in direct relation to temperature. Although germination was completely suppressed at 26 °C, no significant increase in spore mortality was detected. Separate experiments have

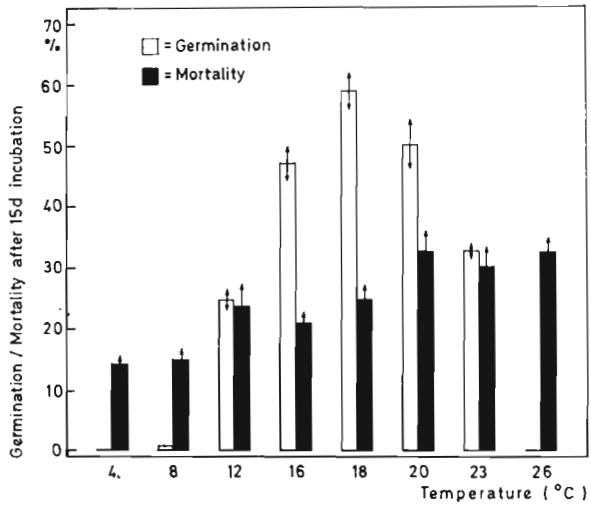
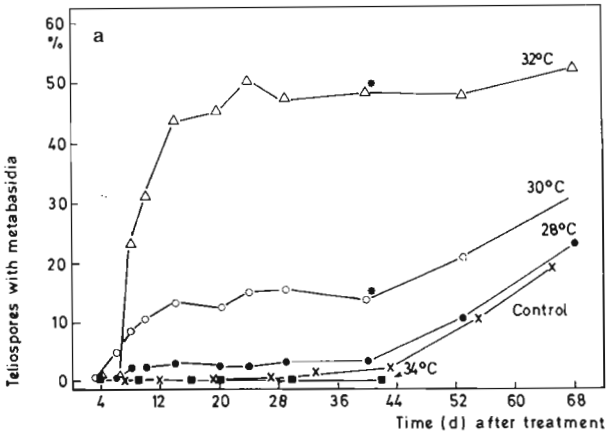


Fig. 4. Effect of temperature on germination and mortality rate of RBR 1 teliospores. Spore age: 8.5 mo (stored outdoors). The arrows indicate the standard deviations of the means



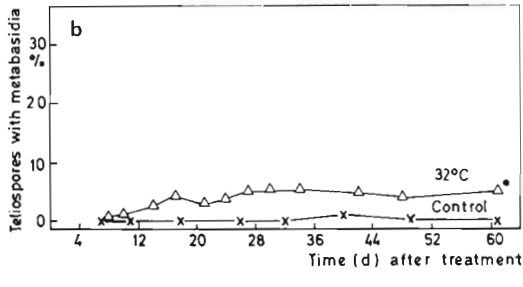


Fig. 5. (a) Germination of SWBR teliospores as a function of temperature treatment. Spores were treated for 4 d or not treated (controls). Spore age: 8.5 mo; (b) Germination of GBR teliospores after heat treatment for 4 d or no treatment (control). Spore age: 17 mo

shown that the thermal death point of bean rust teliospores lies between 33 and 34 °C. The standard deviations shown in Figure 4 are representative of the amount of variation observed in all experiments on teliospore germination.

2.2. Cold treatment

Thirty-five telial cultures were established. Routine germination tests with primary bean leaves showed that teliospores from 23 of the cycled cultures had been activated to germinate. This method invariably resulted in only weak, sporadic germination, and following 9 treatments, over 90 % of the spores in the telial cultures were dead.

2.3. Heat treatment

Following 4 d of treatment at 30 or 32 °C, teliospores of SWBR germinated significantly more than the spores treated at 28 °C or the control

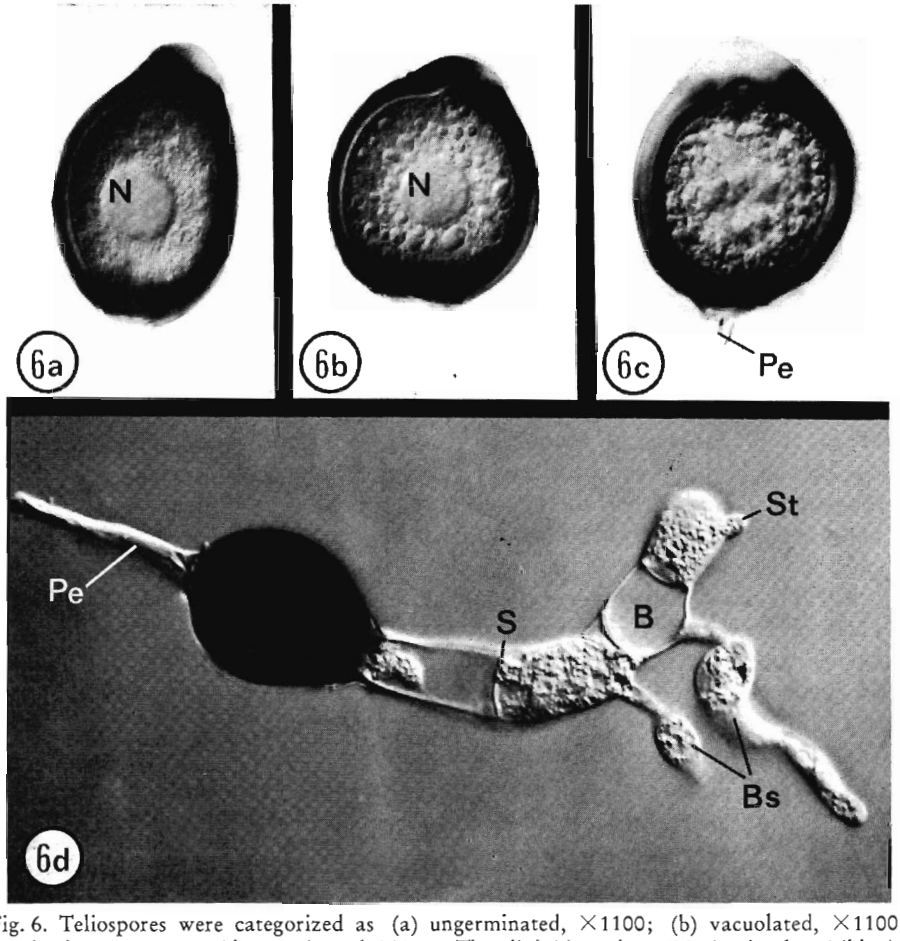


Fig. 6. Teliospores were categorized as (a) ungerminated, ×1100; (b) vacuolated, ×1100; (c) dead, ×1150; or (d) germinated ×800. The diploid nucleus (N) is clearly visible in intact spores

spores (Fig. 5 a). The spores treated at 34 °C were killed. Beginning at 6 wk after the 28 and 30 °C treatments and after plating out of the controls, a gradual increase in germination was observed. This lag increase, however, was not observed with spores treated at 32 °C. In contrast to SWBR, GBR teliospores responded slow and weakly to the 32 °C heat treatment with ~ 5 % germination at 60 d after treatment and the controls did not germinate (Fig. 5 b). Also, no lag increase of germination was observed in GBR for either treated or untreated control teliospores.

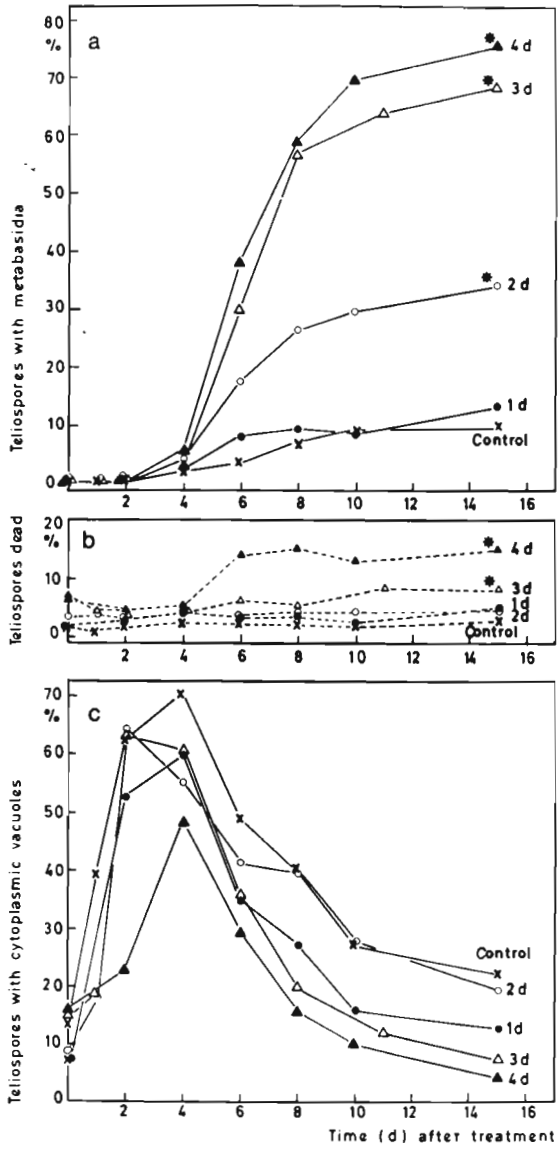


Fig. 7. Rate of germination (a), mortality (b), and vacuolation (c) of SWBR teliospores as a function of heat treatment duration. Spores were treated at 31.6 °C or not treated (controls). Spore age: 16 mo

The effect of treatment duration was determined with spores treated at 31.6 °C for 1—4 d. Spore samples were evaluated as either ungerminated, vacuolated, germinated, or dead (Fig. 6). A direct relationship was found between length of treatment and percentage germination (Fig. 7a). A sharp increase in germination occurred ~ 4 d after the end of the 2, 3, and 4 d treatments and at 15 d the same treatments showed significant differences over the controls. The 3 and 4 d heat treatments caused a significant increase in spore mortality over the controls at 15 d (Fig. 7 b). Vacuolation of the spore cytoplasm increased rapidly reaching a maximum ~ 4 d after the end of each respective treatment as well as 4 d after rehydration of control spores (Fig. 7c). The lowest percentage of spores with vacuoles was observed in the 4 d treatment and the highest percentage in the control spores.

The length of storage at 4 °C prior to the heat treatment markedly influenced the level of activation of teliospore germination in SWBR (Fig. 8 a). Maximum germination (~ 63 %) occurred with spores stored for 24.5 mo. Spores stored for 9.5 mo as well as fresh spores both showed significant increases in germination over the untreated controls. The 24.5 mo control spores germinated better than the fresh treated spores. Heat-induced activation of GBR teliospores was only observed with spores which had been stored for several month at 4 °C (Figs. 5 b and 8 b).

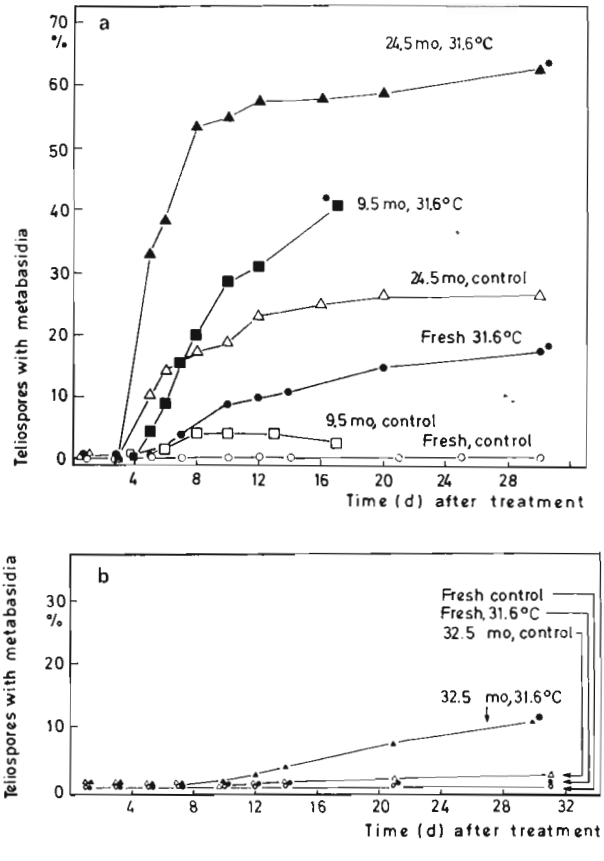


Fig. 8. Effect of heat treatment on germination of fresh versus stored (4 °C) teliospores of SWBR (a) and GBR (b). Spores were treated for 3 d or not treated (controls)

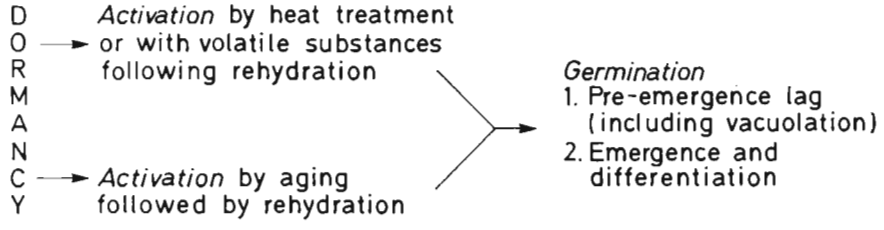
Heat treated spores germinated weakly (~ 2 %) after 30 d incubation in the dark compared to ~ 52 % germination in the light. Furthermore, dark incubation of treated spores proved harmful and led to over 90 % mortality in the spore population.

Numerous attempts to infect primary bean leaves with basidiospores from heat-activated teliospores were either unsuccessful or resulted in low level infections. The basidiospores were not released from the metabasidia. Germinating control spores often effected a higher level of basidiospore infection although, in some cases, the heat-treated teliospores had reached a 5 to 10-fold higher level of germination.

Discussion

The teliospores of bean rust are dormant after formation. Before germination takes place they require an activation period. Following activation, germination is then primarily dependent on (1) the fungal isolate and/or age of teliospores, and (2) the environmental conditions prevailing after rehydration.

To faciliate this discussion the following scheme was developed (see also MENDGEN 1983).



The activation period may range from three days (heat treatment) to four years (refrigerator storage). Water (rehydration) is a necessary external factor that must be present in order for germination to occur. The germination process may be divided into (1) a pre-emergence lag period and (2) an emergence and differentiation period during which metabasidia appear and basidiospores develop. At 18 °C, a 3—5 d pre-emergence lag period was observed for SWBR after the end of each heat or seedling treatment. The length of the lag period remained relatively constant regardless of the treatment given, the age or level of germinability of the teliospores. The length of the lag period was influenced slightly by incubation temperature, but never eliminated. Seventy reports concerning the lag period of germinating teliospores were found in the literature. The results vary extremely from 2—4 in *C. fusiforme* (SNOW 1968) and *G. juniperi-virginianae* (PADY and CRAMER 1971) to 3 d in *P. graminis* (LAMBERT 1929) or 6—7 d in *Uromyces fabae* (KAPOORIA 1971). In *P. graminis* (LAMBERT 1929), the length of the pre-emergence lag period was directly related to the time overwintered outdoors. Similar to bean rust, POWERS and RONCADORI (1966) showed that the lag period in *C. fusiforme* remained constant with increasing spore age.

1. Effect of aging

The rate of germination and mortality of stored bean rust teliospores was dependent on storage conditions. Spores stored in a refrigerator increased very slowly in germinability and were still viable after 4 years. In contrast, spores stored outdoors became rapidly germinable, but after ~ 1 year the entire spore population was dead. The rather sudden death of the teliospores after 10—12 mo may be due to warm incubation conditions during the summer months. Particularly interesting is the relationship between weather conditions and teliospore germinability. It appears significant that the sharp increase in teliospore germinability observed *in vitro* between January and March coincide with the coldest and wettest months of the winter-spring seasons. However, *in vivo,* the cold outdoor temperatures from January to May prevented germination in the field.

HARTER *et al.* (1935) conducted a storage experiment with field grown teliospores of bean rust. Following ~ 7 mo cool storage the spores were tested for germinability. The authors recorded 50—60 % germination after incubating the spores on water drops for 21 d (temperature not specified). This level of germination is comparable with that observed in RBR 1 after 7—8 mo outdoor storage.

2. Effect of temperature

Freezing in combination with alternate wetting and drying is an often used method to activate teliospores to germinate (see GOLD and STATLER 1983, MENDGEN 1983). This method is technically very simple and has been relatively effective with most tested species. Teliospores of bean rust responded unsatisfactorily to the cold treatments. Weak, sporadic germination and high mortality rates were the usual results and pycnia developed only infrequently after inoculation trials. GROTH and MOGEN (1978) were also unsuccessful in breaking teliospore dormancy of bean rust using similar methods. In fact, they observed that freezing teliospores caused a longer dormancy than usual (J. V. GROTH, University of Minnesota, pers. comm.).

The use of heat to activate teliospore germination has apparently been only randomly investigated (MANEVAL 1922, MISRA and SHARMA 1964). In both reports the heat treatments proved harmful and led to ~ 90 % reduction in the germinability of the treated spores. In bean rust the best activation results were obtained with temperatures between 30—32 °C for periods of three to four days. Longer durations inevitably resulted in an increase in spore mortality. All experiments with higher activation temperatures (ranging from 35—60 °C) for relatively short durations (10 sec to 3 min) proved either ineffective or detrimental. Preliminary experiments with dry-heat treatments (30—40 °C for 5—10 d) induced a small increase in germination (MENDGEN, unpublished). However, additional work is necessary to verify these findings. KLISIEWICZ (1977) recently studied the effect of heat treatment on teliospore germination in *P. carthami.* These results showed that temperatures above 30 °C for two days significantly reduce spore germinability. It may be assumed that these reductions were primarily a result of spore mortality.

Significant differences between the isolates SWBR and GBR were observed in their response to heat treatments. Whereas the activation of GBR was possible only with stored teliospores, both fresh and stored teliospores of SWBR were receptive to heat activation. In SWBR, the level of activation, with temperature and treatment duration held constant, was directly related to spore age. These differences between GBR and SWBR may be in part related to the origin of these isolates. SWBR was collected in the field from a natural urediniospore population that overwinters each year as teliospores. The GBR isolate originated from a population that has been propagated asexually for ~ 20 years as urediniospores in the greenhouse. Although GBR produces teliospores, their ability to germinate has been largely lost.

The greatest problem associated with the heat treatment was the low level of basidiospore infection after inoculation with heat activated teliospores. This low level may be due to a disruption in the basidiospore release mechanism.

The site and mechanism of heat activation has not been clearly demonstrated in any fungal system. At present the most convincing hypothesis is based on the biochemical work of COTTER and co-workers (see COTTER 1981), HOHL *et al.* (1978), MAHESHWARI and SUSSMANN (1971), and THEVELEIN *et al.* (1979). They suggest that a conformational change of proteins in the plasma membrane triggers the germination process.

Cytoplasmic vacuolation commonly occurs during rehydration and germination of fungal spores (LONGO *et al.* 1979, MIMS 1981, see GOTTLIEB 1978). In bean rust the occurrence and disappearance of cytoplasmic vacuoles was independent of spore age, germinability and the treatment applied. Interestingly, the increase in vacuolation in treated spores first began after the end of each respective heat treatment. This observation supports the hypothesis that teliospores remain in a state of prolonged dormancy during the length of the heat treatment.

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