REPRODUCTIVE POTENTIALS OF RACES 15B-1 (CAN.) AND 56 OF WHEAT STEM RUST

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ABSTRACT

Race 56 of wheat stem rust, Puccinia graminis Pers. f. sp. tritici Erikss. & Henn., was found to have superior competitive ability than race 15B-1 (Can.) when they were cultured in mixtures on the varieties Little Club, Red Bobs, and Marquis for 11 generations. The superiority of race 56 was most evident at high temperatures (20° and 25°). Race 15B-1 (Can.) was a much better competitor at 15°C than at 20° and 25°C.

Relative competitive abilities were found to be influenced by the density of pustules on infected leaves. On heavily infected plants of Little Club and Red Bobs at 15° and 20°C race 15B-1 (Can.) usually predominated over race 56 but on lightly infected plants race 56 predominated.

The germinability of urediospores of race 15B-1 (Can.) was slightly superior to race 56 on water agar but there was no difference on wheat leaves. There was not much difference in the longevity of spores of the two races. Spores of both races lost viability quickly at 25°C.

The successful rate of infection by single spores on Little Club seedlings was the same for races 15B-1 (Can.) and 56. The infective ability of race 56, however, was generally higher than that of race 15B-1 (Can.) on the wheat varieties Little Club, Red Bobs, Marquis, and Mindum. Marquis wheat was generally the most readily infected by the both races. Generally, the higher the temperature at which inoculated seedlings were kept, the fewer pustules developed on the plants.

The rate of growth of pustules on Little Club wheat grown at 15° and 20°C was determined by measurement with a microscope. During the early stages of rust development, the pustules of race 56 grew faster than those of race 15B-1 (Can.). Pustules of race 15B-1 (Can.), however, grew more rapidly in later stages and were larger than those of race 56 in the final stage of rust development.

Pustules of both races were smaller on heavily infected plants than on lightly infected plants.

The incubation period of race 56 was shorter than that of race 15B-1 (Can.) at 15° and 20°C. Incubation periods were shorter at 20°C than at 15°C.

Race 56 produced more urediospores more rapidly than race 15B-1 (Can.) at 15°, 20°, and 25°C.

There was no antagonistic effect between races 15B-1 (Can.) and 56 in this experiment.

The reproductive potentials of races 15B-1 (Can.) and 56 of wheat stem rust are discussed.

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INTRODUCTION

Physiologic races of various plant pathogenic fungi continuously vary in prevalence in nature. It is well-known that the introduction of new resistant varieties plays an important part in bringing about such changes. But it is also well-known that the prevalence of physiologic races changes in periods when the varieties of the host crop are static. Alterations in race prevalence that cannot be attributed to the reaction of crop varieties must be brought about by other environmental factors interacting with the capabilities of the races to develop and sporulate. Little is known about the these interactions and their effect on the competitive abilities of races in nature.

Changes in the prevalence of races 15B-1 (Can.) and 56 of wheat stem rust, Puccinia graminis Pers. f. sp. tritici Erikss. & Henn., illustrate many aspects of the problem. Race 56 was first found in Canada in 1928. It became the predominant race in 1934 and remained so until 1949 despite the widespread use of varieties resistant to it after 1935. In 1950, a new race, 15B, suddenly displaced it for the obvious reason that 15B could attack all the resistant varieties of bread wheat and durum wheat grown in the Great Plains region of North America at that time. In 1953, the variety Selkirk, with resistance to both races, was released and soon became the predominant variety in the rust area of Western Canada and in the spring wheat area of north-central United States.

Soon after the introduction of Selkirk the prevalence of race 15B declined and race 56 again became predominant despite the advantage of broader host range favoring race 15B.

The ability of the cereal rusts to change and produce new races, some of which can attack widely grown resistant varieties, poses plant breeders and pathologists with a continuing problem in controlling the cereal rusts. But new races that appear to be equally threatening from the standpoint of virulence do not have equal abilities to increase and menace crops. Several races, such as 29-1 (Can.), 15B-3 (Can.) and 15B-5 (Can.) can attack Selkirk but they were unable to develop and threaten crops in the Great Plains region of North America. Nevertheless, when they were discovered they were viewed as serious potential threats and breeding programs were initiated to counteract them. If the factors, other than virulence, that govern the prevalence of races in the field were understood much time and effort could be saved. These factors, therefore, have great practical importance.

A knowledge of how environmental conditions affect the competitive abilities of different rust races would be helpful, also, in understanding the epidemiology and ecology of the rusts. Studies on the competitive ability of rust races reported in the literature have been concerned mainly with the ability of races to increase at the expense of other races in mixed uredial infections over several generations. Little is known about the factors that make one race a better competitor than another in a mixture.

This investigation was undertaken to elucidate some of the

factors that may have been responsible for the increase of race 56 and the decline of race 15B after 1953. The factors governing the competitive ability of races in mixed uredial infections under artificial conditions can be broadly classified into two groups - 1) the inherent capabilities of the races or internal factors and 2) environmental conditions. The internal factors include urediospore viability, infective capability, rate of growth, and sporulating capacity. Environmental factors include host variety, infection density, and temperature and other meteorological conditions. The inherent capabilities of races 15B-1 (Can.) and 56 of wheat stem rust were compared under several different environmental conditions to learn what factors favored one race or the other and thus explain the marked changes in their prevalence in the field.

REVIEW OF LITERATURE

Studies on the relative survival ability in mixed infections of races of pathogenic fungi and studies on the reproductive potential of cereal rust races have been reported in the literature. In this review, only papers considered relevant to this investigation will be discussed.

In studies on competitive ability in wheat stem rust, P. graminis f. sp. tritici, Watson (59) found that race 34 always grew well and maintained itself, or increased, in percentage of the mixture when associated with races 17, 19, 56, and 147, whereas race 147 was always virtually eliminated from such mixtures after several uredial generations. He suggested that the amount and character of each race in mixture, the effect of temperature on the fungus, and the variety on which the mixture was cultured might be responsible for the changes.

Loegering (38) reported that, in a mixture of races 17 and 56 on the wheat varieties Fulcaster and Little Club, race 17 became predominant by a wide margin, while on Ceres it predominated only slightly. In a mixture of races 17 and 19, on Fulcaster and Little Club, race 17 predominated after a very few generations, while on Mindum race 17 predominated only slightly after six generations.

Bromfield and Broyles (3) found by studying survival rates in mixed cultures that the survival ability of many races might be determined by comparing races in mixtures with one or more marker races.

In leaf rust of wheat, Puccinia recondita Rob. ex Desm., Irish (23) found that race 58 is the weakest competitor of races 9, 15, 58, and 126 on the variety Cheyenne.

Hassebrauk (19) reported that race 52 of leaf rust predominated over race 20 in mixed infections on Michigan Amber for 50-60 uredial generations.

In studying mixtures of races of Phytophthora infestans (Mont.) de Bary, Black (1) found that the wider the host range of a race, the less prolific it was on varieties susceptible to many races, and the lower its survival values in competition with races with narrower host ranges. These results were supported by Thurston and Eide (57, 58) in studying P. infestans. They reported that an isolate from the resistant variety Cherokee lacked survival ability when grown on the susceptible variety Cobbler in mixtures with a field isolate.

Thurston (56) found that race 0 of P. infestans predominated or entirely displaced the other races with which it was mixed after perpetuation of the mixture on susceptible potato clones for 2-9 generations. When compared singly, isolates of race 0 were usually more infectious than the other races. He concluded that survival ability is the result of a complex of factors, and suggested that these factors may be influenced by the various interactions of host, parasite, and environment; and probably include ability of a fungus to overseason; to grow after overseasoning; to sporulate; to survive dissemination until arrival on a susceptible host; to germinate rapidly; and finally to penetrate and infect the host.

Rodenhiser and Holton (46), in studying differences in capacity for survival in interspecific and inter-race mixtures of Tilletia caries (DC.) Tul. and/or T. foetida (Wallr.) Liro, found that the species and races of the bunt fungi differ in their ability to develop in a susceptible host in mixed populations. They reported that no explanation can be offered for the demonstrated differential ability of species and races of T. caries and T. foetida to survive passage through the host in combination with each other. Rate of spore-germination may be at least a contributing factor in some cases. Antagonistic effects on mycelial growth apparently had no influence.

Cassell (7) studied the effect of temperature on urediospore germination and germ tube development of several races of wheat stem rust. He found that, in general, 20°C was most favorable for spore-germination. The races did not behave alike. Spores of race 34 germinated better than those of the other races over a wide range of temperature, but germ-tube growth was poorest at 20°C. Germ-tubes of race 56 developed faster than those of all other races at 20°C, closely followed in this respect by race 11 and race 38. He concluded that on the basis of spore-germination, race 36 was one of those best adapted to high temperature and was only partially tolerant to cold, race 56 was next to race 36 in its ability to develop at high temperature and was the least adapted to cold, and races 38 and 11 were best able to tolerate low temperature.

Manners (39), in studying Puccinia glumarum (Schm.) Erikss. & Henn., found that urediospores of race 2 germinate less well than

those of races 5 or 8, other races being intermediate, and that the optimum temperature for spore-germination of race G (isolated from Dactylis glomerata L.) is 22.5°C, that of all other races is 10-13°C.

Line and Bugbee (37) compared the germination ability of isolates of race 15B of wheat stem rust selected at low incubation temperature (4-5°C.) for more than 20 generations and nonselected isolates. At 3-5°C, urediospores of selected isolates germinated sooner, produced longer germ tubes, and were higher in percentage of germination than spores of nonselected isolates of races 15B and 56. At 20-25°C, urediospores of nonselected isolates germinated better. When urediospores of isolates selected at 4-5°C were transferred for 4 and 8 generations at 20-25°C, they germinated better at 3-5°C than spores of isolates always transferred at 20-25°C, but less well than spores of selected isolates always transferred at 4-5°C.

In studying infectibility of hosts to rust, Hayden (20) found that the spread of race 15B differed on the wheat varieties Lee, Marquis, Mida, Carlton, Nugget, and Sentry. Rust severity reached 35-50% in an area approximately 3 feet in diameter on Lee but the area of spread was more extensive and severity was greater on Marquis and Mida. Determinations of temperature range or moisture requirements for infection of seedlings of individual varieties which might account for differences in infectibility and rate of development of rust to epidemic proportions were inconclusive.

In studying the effect of temperature on the development of rust races, Melander (40) found that physiologic races of wheat

stem rust differed in ability to produce uredia at low temperature. At 0-1°C, race 36 produced normal uredia readily, races 15 and 35 produced only a few minute pustules.

Johnson and Newton (26) showed that physiologic races of the cereal rusts differ considerably in their response to high temperatures, and the higher the temperature at which the host plants were kept, the fewer pustules developed on the plants. Cassell (6), in comparative tests between races 36 and 56 of wheat stem rust on Ceres wheat, found great difference at different temperatures. Race 36 caused the heaviest infection at moderate to low temperatures, while race 56 caused the heaviest infection at moderate to high temperatures. He also reported that mycelia of race 15B survived in the host for 85 days at low temperatures, and for 42 days at high temperatures.

Yarwood (60) first reported acquired immunity to rust after studies in which he inoculated plants a second time with the same or with different rust species. He stated that a gaseous metabolite of the pathogen is responsible for immunization, and that immunization is restricted to the germination and penetration phases of the infection. He found that the tissue adjacent to old uredial infections of bean rust, Uromyces phaseoli (Rebent.) Wint. on Phaseolus vulgaris L., was not infected by the second inoculation. The zone of inhibition was wider distally than proximally from the infected area, and its width varied directly with the age of the first infection. He concluded that a gaseous substance formed by U. phaseoli is toxic to the germinating spores of certain rusts but

is not toxic to certain other plant pathogens.

In double inoculations with different rusts, Yarwood (61) found that when adequate dosages of urediospores of U. phaseoli were placed on sunflower leaves before inoculation of the leaves with Puccinia helianthi Schw., or along with the inoculum, the sunflower leaves were protected from infection. Johnston and Huffman (34) pointed out that on leaf rust susceptible wheat seedlings inoculated with urediospores of oat crown rust prior to inoculation with the wheat leaf rust, the leaf rust pustules were fewer in number and of a different infection type than were those on similar plants inoculated only with the leaf rust. They suggested that local antagonism may be one of contact inhibition by the action of substances produced by the latent mycelium of an organism that was not able to establish itself parasitically, or that it may result from a reduction in the number of possible infection courts caused by killing or plugging of many of the stomata.

MATERIALS AND METHODS

Isolates of races 15B-1 (Can.) and 56 of wheat stem rust, P. graminis f. sp. tritici, obtained from rust collections made in Western Canada and a grayish-brown isolate of race 15 obtained in hybridization studies in the greenhouse, were supplied by Dr. G. J. Green, Canada Department of Agriculture Research Station, Winnipeg. Monourediospore cultures were established and used in this study to avoid errors resulting from the use of cultures consisting of more than one genotype. The cultures were established by picking up a single spore on a sterile needle under a microscope and placing it on a seedling leaf of the wheat variety Little Club. Seedlings inoculated in this way were incubated under lantern chimnies in a growth chamber at 20°C for 24 hours. The lantern chimnies were then removed and the results of inoculation were observed 10 days later. The number of successful infections was 2.3 per cent for race 15B-1 (Can.) (15 infected plants/640 plants inoculated), and also 2.3 per cent for race 56 (15 infected plants/655 plants inoculated). The percentage of single spore infections of the grayish-brown isolate was not calculated. The grayish-brown culture was used, in addition to races 15B-1 (Can.) and 56, because in studying competitive ability in spore-mixtures, uredia of races 15B-1 (Can.) and 56 are not distinguishable on varieties susceptible to both races, while the grayish-brown race can be distinguished from races 15B-1 (Can.) and 56 on the susceptible varieties. All the cultures were grown on Little Club seedlings in different growth chambers to avoid contamina-

tion, and occasionally their purity was confirmed by testing on the differential host varieties.

Seeds of the wheat varieties Little Club, Red Bobs, Marquis, Mindum, Spelmar, and Arnautka were obtained from stocks at the Canada Department of Agriculture Research Station, Winnipeg. The varieties Little Club, Red Bobs, and Marquis are susceptible to the three rust cultures used but Mindum, Spelmar, and Arnautka are resistant to race 56 and susceptible to race 15B-1 (Can.) (Table 1).

Table 1. Rust reaction of five wheat varieties to three races of stem rust.

Race	Little Club	Marquis	Red Bobs	Mindum	Arnautka
15B-1 (Can.)	4	4-	4	4=	4=
56	4	3+	4	1=	1=
15 (grayish-brown mutant)	4	4-	4	4=	4=

The seedlings used in the experiments were grown in 4 inch clay pots in a growth chamber at 20°C, and in a few cases at 25°C, at the Canada Department of Agriculture Research Station. Temperatures in the growth chambers varied ± 1°C. Relative humidity was maintained at about 40% (20-60%). Light, supplied 16 hours per day by cool white fluorescent tubes, was about the same intensity in all growth chambers.

The varieties Little Club and Red Bobs were used because they are completely susceptible to the races used, while Marquis was slightly more susceptible to race 15B-1 (Can.) than to race 56. Mindum, Arnautka, and Spelmar were used to determine the proportions of races 15B-1 (Can.) (susceptible) and 56 (resistant) in urediospores harvested from mixed infections.

In most experiments, seedlings in the first leaf stage were inoculated by spraying with a suspension of urediospores in water containing 1 per cent polyoxyethylene sorbitan monolaurate (Tween 20). The addition of Tween 20 was necessary to suspend the spores uniformly in the water and to produce a uniform infection on the seedlings. The suspensions were prepared by adding weighed quantities of urediospores of the different cultures to the water-Tween 20 solution. Throughout the tests care was taken to apply approximately the same amount of suspension to each plant although the amount was not measured. The seedlings inoculated were incubated for 24 hours under glass lamp chimnies in the growth chambers used for the particular experiment and then the lamp chimnies were removed. A second method

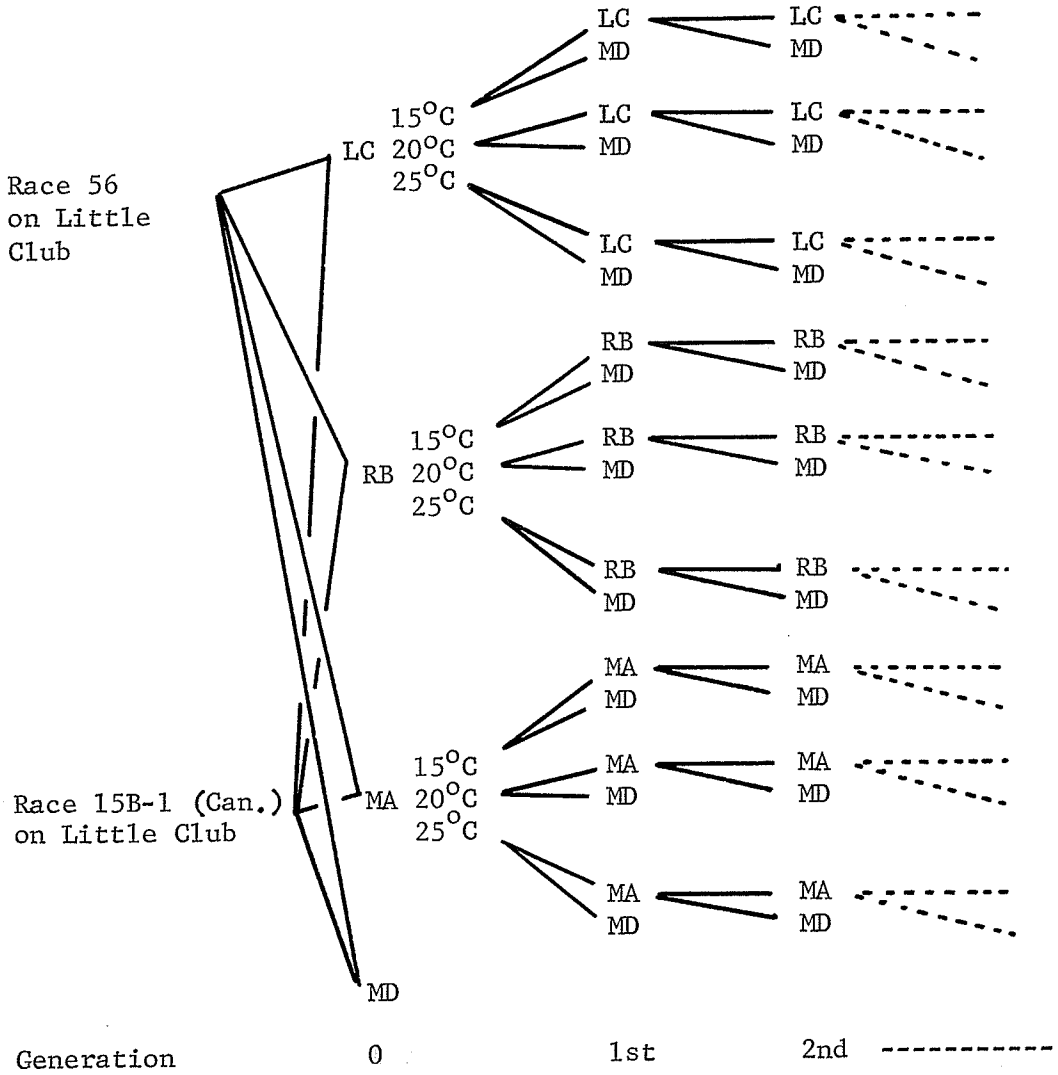
of inoculation, used mainly for increasing cultures, was the application of spores to seedlings with carefully washed fingers. Seedlings were sprayed with water containing 1% Tween 20, and the spores were applied by drawing the moistened leaves between carefully washed thumb and forefinger. The seedlings were incubated as described above.

Tests on the effect of polyoxyethylene sorbitan monolaurate on spore germination showed no difference between germination in a solution of 1% Tween 20 and in water.

The urediospores of single spore cultures used in each experiment were grown on seedlings of Little Club wheat at 20°C. In each test of competitive ability, seedlings of Little Club, Red Bobs, Marquis, Mindum, Spelmar and/or Arnautka were inoculated with the same 1% Tween 20 suspension of spores prepared with 25 mgs of urediospores of the races being compared per 100 cc. Subsequent generations were produced by collecting spores from the mixed infections on each variety by shaking the seedling leaves over a sheet of cellophane and inoculating new seedlings with the mixture (Figure 1a). The spores from the mixed infections were collected 18 days after inoculation at 15°C and 14 days after inoculation at 20° and 25°C.

Experiments on the effect of pustule density on competitive ability were carried out in a similar manner (Figure 1b). A suspension of 40 mgs of urediospores of each race in 50 cc of 1% Tween 20 solution was used to produce heavy infections (over 100 infections

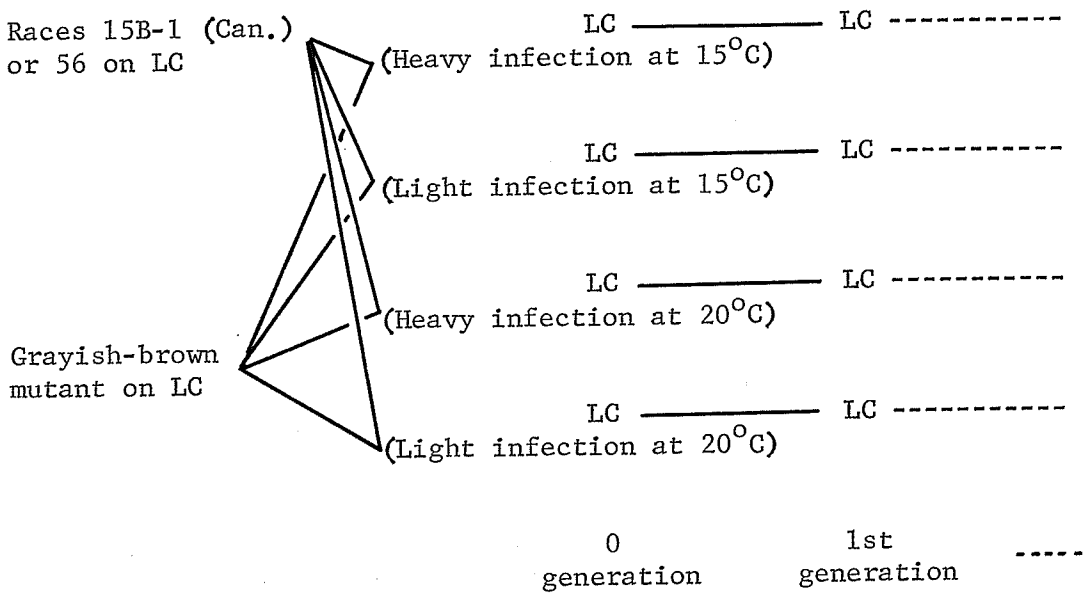
Figure 1a. Serial inoculation diagrammed



Note: LC: Little Club
RB: Red Bobs
MA: Marquis
MD: Mindum

per leaf) and 8 mgs of spores of the races in 50 cc of suspension of 1% Tween 20 was used to produced light infections (less than 10 infections per leaf).

Figure 1b. Serial inoculation diagrammed.



The relative survival of races 15B-1 (Can.) and 56 in a mixture were determined after each generation by infecting the wheat varieties Mindum, Spelmar and/or Arnautka with urediospores from the mixed infections. These varieties are resistant to race 56 and susceptible to race 15B-1 (Can.). The number of resistant and susceptible infections, therefore, indicated the proportion of each race in the mixture. Tests with mixtures in which the proportion of each race was known had previously demonstrated that this was a reasonably accurate assay method (53, 55).

Urediospore color mutants have an advantage in studying competitive ability in a mixture, because uredia of a mutant are distinguishable from those of normal colored races on susceptible varieties. Therefore, it is not necessary to use differential hosts such as Mindum, Spelmar, and Arnautka as in studying competition between races 15B-1 (Can.) and 56. In studies of competition between a grayish-brown mutant and normal colored races 15B-1 (Can.) and 56, the number of infections of each race was counted directly. The experimental procedure was the same as that mentioned above (see Figure 1a).

Spore viability was determined by sparsely seeding fresh urediospores of races 15B-1 (Can.) and 56 on 1% water agar in petri dishes which were kept in chambers at 5, 10, 15, 20, 25, 30, and 35°C. In another germination test, the spores were seeded on the undersurface of detached wheat leaves which were placed on moist filter paper in petri dishes kept at 15°, 20°, and 25°C. In both experiments, percentage of germination was determined by counting the

germinated spores under a microscope at 6 to 8 hours after seeding the spores.

To investigate the longevity of urediospores of races 15B-1 (Can.) and 56, fresh urediospores of both races were kept separately in petri dishes which were placed in growth chambers at 15°, 20°, and 25°C. The germinability of the spores was tested on 1% water agar after 0 to 40 days of storage. At the same time, 2 mgs of fresh urediospores of each race were sealed separately in evacuated glass tubes by means of vacuum drying apparatus. The sealed tubes were kept in the growth chambers. The spores in the tubes were tested for germination on 1% water agar after 0, 7, and 42 days of storage.

To investigate the infectivity of races 15B-1 (Can.) and 56, 27 pots of seedlings of the varieties Little Club, Red Bobs, Marquis, and Mindum were inoculated separately with 11 or 20 mgs of fresh urediospores of each race suspended in 50 cc of 1% Tween 20 solution. The plants were kept in growth chambers at 15°, 20°, and 25°C. The number of infections on the wheat varieties were counted 12 days after inoculation.

The growth rate of pustules of races 15B-1 (Can.) and 56 was compared by observing when infections of each race first ruptured the host epidermis, and the rate of increase in the size of pustules of each race.

The "opening" of the pustules was determined by counting the number of opened pustules on Little Club leaves, which were infected heavily (more than 100 infections per leaf) and lightly

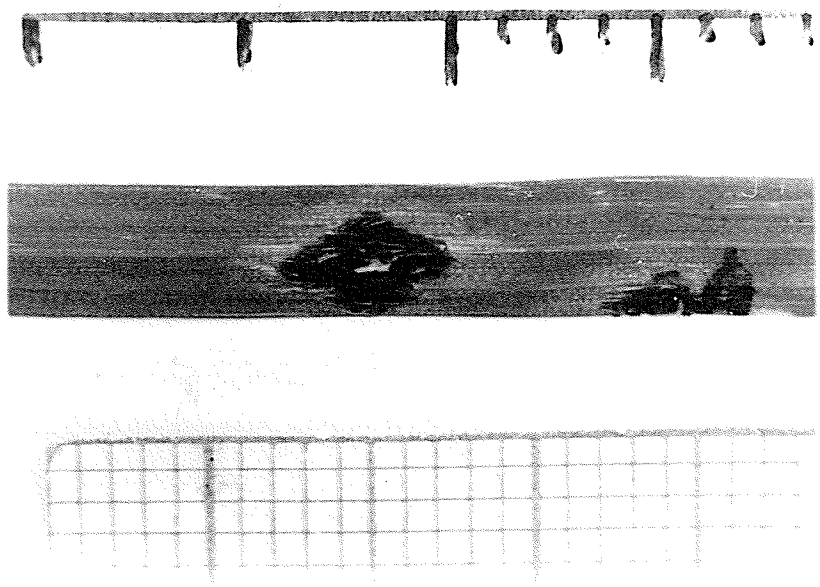
(less than 10 infections per leaf) with each race at 15° and 20°C, every day from 5 days after inoculation.

The pustule size of the races was compared by removing infected leaves of Little Club 8 and 10 days after inoculation, and measuring the length and width of the pustules on the undersurface of the leaves by microscopic examination using an ocular micrometer. The size of each uredium was estimated by means of the formula: $\frac{1}{4}$x length x width x π (21). The growth rate of the pustules was determined by this method and by a photographic method. In the photographic method a close-up photograph of 5 pustules of each race on leaves of Little Club (1 or 2 infections per leaf) was taken every other day. A ruler was placed beside each pustule when photographed. The area of each pustule was determined from positive enlargements using a planimeter (Figures 2a and 2b) and the ruler in each photograph.

The effect of infection density on growth rate of pustules was also investigated by measuring the size of pustules on leaves infected heavily (more than 100 pustules per leaf) and lightly (less than 10 pustules per leaf) with races 15B-1 (Can.) and 56 at 9 and 14 days after inoculation.

To determine the growth rate of pustules in mixed infections of the normal colored races and the grayish-brown mutant, seedlings of Little Club were inoculated with mixtures of urediospores in the usual way. The size of the pustules of each race on the leaves was estimated by microscopic measurement, as described above, at 10 and 12 days after inoculation. At the same time,

Race 15B-1 (Can.)



Race 56

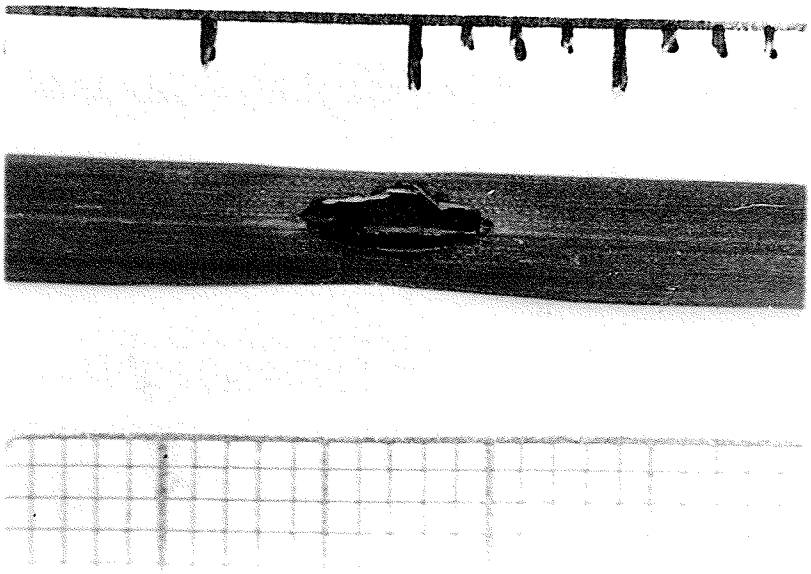
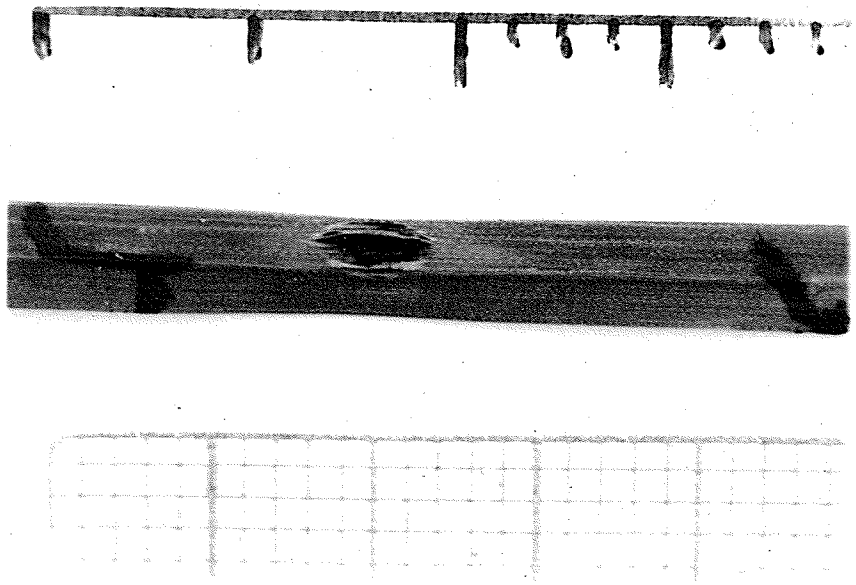


Figure 2a. Photographic measurement of pustules of races 15B-1 (Can.) and 56 fifteen days after inoculation at 20°C. The top scale is in inches, the lower scale in mm.

Race 15B-1 (Can.)



Race 56

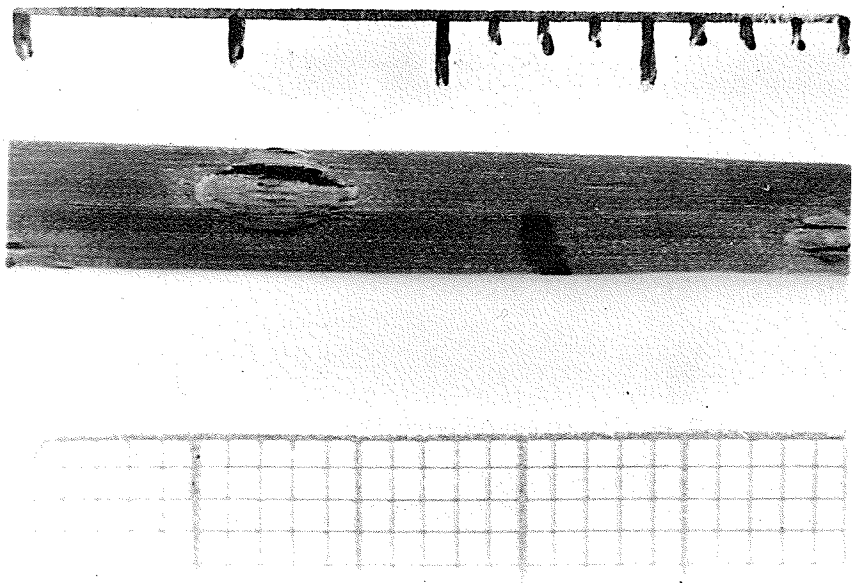


Figure 2b. Photographic measurement of pustules of races 15B-1 (Can.) and 56 fifteen days after inoculation at 15°C. The top scale is in inches, the lower scale in mm.

pustule densities on the same leaves were recorded by counting the number of infections per leaf.

Spore-producing capability is probably one of the most important factors influencing the rate of spread and development of a race. The spore-producing ability of races 15B-1 (Can.) and 56 was compared by inoculating 8 pots of seedlings of each of the varieties Little Club, Red Bobs and Marquis with 7 or 8 mgs of fresh urediospores of each race in 80 cc of 1% Tween 20 solution. In a second trial 6 pots of seedlings of Little Club were inoculated with 2 mgs of urediospores of each race in 20 cc of solution. Thirteen days after inoculation the urediospores produced on the seedling leaves by each race were carefully collected on a sheet of cellophane by shaking the plants and weighed. At the same time, the number of uredia on the same leaves were counted.

Since any differences in competitive ability found by the methods used in parts of this study might be caused by an interaction between the races, a simple test for antagonism between races 15B-1 (Can.) and 56 was carried out. Eight pots of seedlings of the variety Little Club and 12 pots of seedlings of Mindum wheat were inoculated with 6 mgs of urediospores of each race separately in 50 cc of 1% Tween 20 solution. At the same time, 14 pots of Mindum seedlings were inoculated with a mixture of urediospores of races 15B-1 (Can.) and 56 (4.2 mgs of each race). The plants were incubated under lamp chimnies for 24 hours at 15° and 20°C. Afterwards, the seedlings inoculated with a single race were allowed to dry and were again inoculated with the same amount of spore suspension of the other race.

Time between 1st and 2nd inoculation was 24 or 48 hours (Table 18). Twelve days later the number of infections of races 15B-1 (Can.) and 56 on Mindum leaves was counted. Fifteen days after inoculation the urediospores on the infections on Little Club were collected and used to inoculate Mindum seedlings. The number of infections of both races on the Mindum leaves was counted 12 days after inoculation.

EXPERIMENTAL RESULTS

The first stage of the investigation was to determine whether differences in the competitive abilities of races 15B-1 (Can.) and 56 could be detected. If any differences could be found an explanation for them could be sought by comparing the races for spore viability, infective ability, growth rate, and spore producing capability. The experimental results are presented here in this order.

Competitive Ability

i) Races 15B-1 (Can.) and 56

The competitive ability of races 15B-1 (Can.) and 56 was investigated by mixing equal amounts (12.5 mgs) of urediospores of each race and using the mixture to inoculate seedlings of Little Club, Red Bobs, Marquis, Mindum, and Spelmar wheat. The seedlings were incubated and grown in growth chambers at 15^{o}, 20^{o}, and 25^{o}C. Fourteen and 18 days later the spores produced were collected and used to inoculate the same host varieties. The experimental procedure is shown in Figure 1a. The experiment was carried out in duplicate. The combined data (Table 2 and Figures 3 to 5) show that at 20^{o}C and 25^{o}C race 56 quickly became predominant and after 5 generations race 15B-1 (Can.) was nearly eliminated from the mixtures. The results were almost the same on all three host varieties. Apparently at these temperatures on susceptible varieties race 56 is a much better competitor than race 15B-1 (Can.).

Table 2. Survival of races 15B-1 (Can.) and 56 grown in mixtures[1] on three host varieties for 7 generations at 15°, 20°, and 25°C.

Generation	Temp. (°C)	Number of infections		
		Little Club 15B-1 : 56 (Can.)	Red Bobs 15B-1 : 56 (Can.)	Marquis 15B-1 : 56 (Can.)
1	15	103 : 216	151 : 269	130 : 252
2	"	243 : 412	304 : 521	322 : 376
3	"	200 : 230	269 : 245	298 : 292
4	"	283 : 227	291 : 150	213 : 152
5	"	462 : 423	396 : 267	521 : 370
6	"	218 : 129	259 : 144	161 : 101
7	"	367 : 237	311 : 209	313 : 161
1	20	212 : 994	183 : 651	234 : 953
2	"	87 : 410	83 : 508	176 : 861
3	"	36 : 524	98 : 512	85 : 616
4	"	11 : 323	45 : 644	49 : 778
5	"	16 : 884	27 :1173	28 : 524
6	"	8 : 553	20 : 723	30 : 772
7	"	20 :1727	27 :1852	59 :1707
1	25	145 : 713	129 : 475	106 : 226
2	"	13 : 185	29 : 571	11 : 490
3	"	21 : 346	28 : 234	78 : 487
4	"	1 : 239	1 : 150	26 : 452
5	"	1 : 280	11 : 218	1 : 138
6	"	1 : 196	0 : 136	6 : 300
7	"	0 : 459	0 : 571	3 : 603

1) The proportion of races 15B-1 (Can.) and 56, respectively, in the original uredisopore mixtures as indicated by assay on Mindum were: 15°C - 1381 : 1632; 20°C - 603 : 1186; 25°C - 844 : 1606.

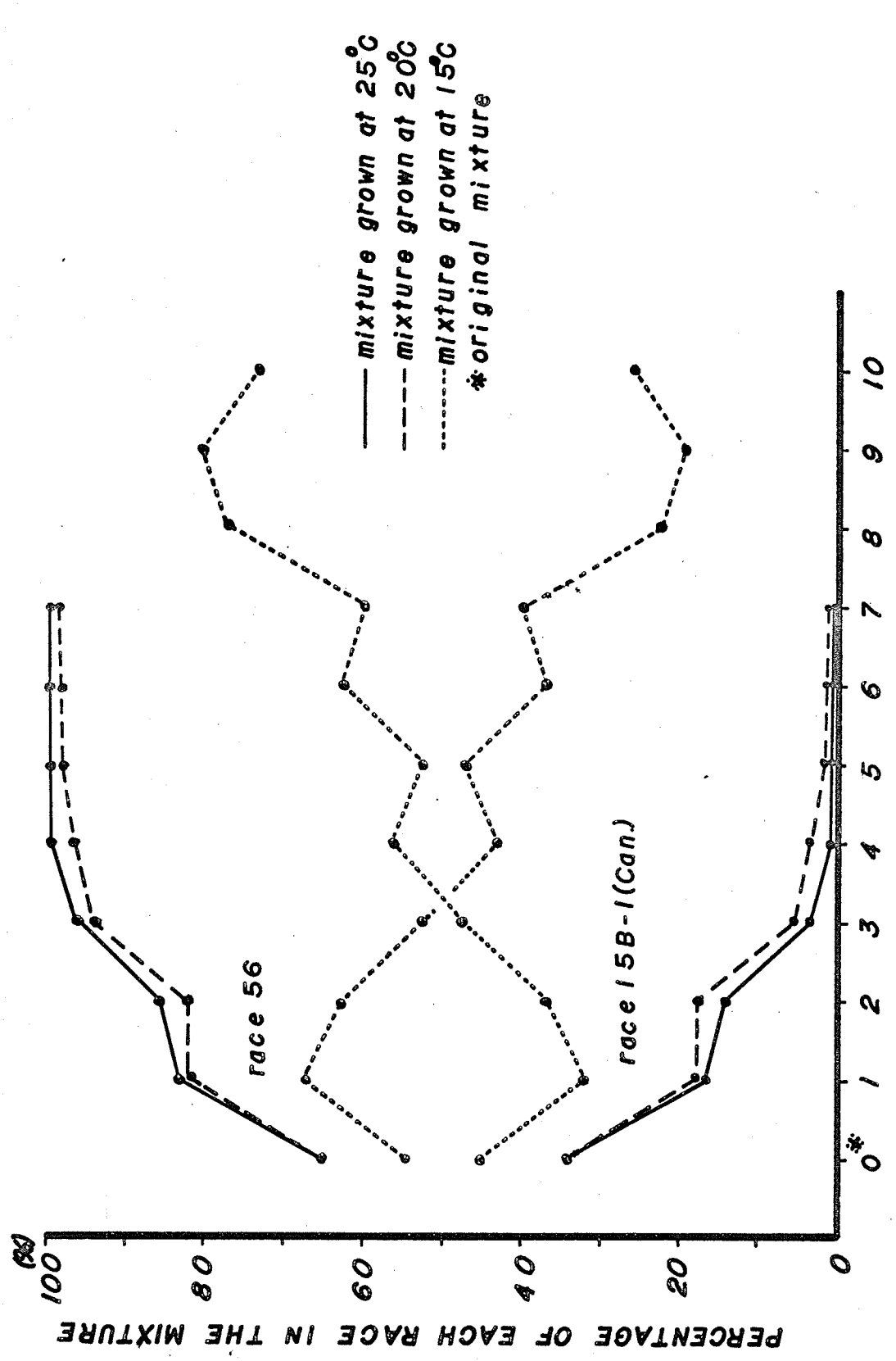


Figure 3. Percentage of survival of races 15B-1 (Can.) and 56 grown in mixtures on the variety Little Club for 10 generations at 15°, 20°, and 25°C.

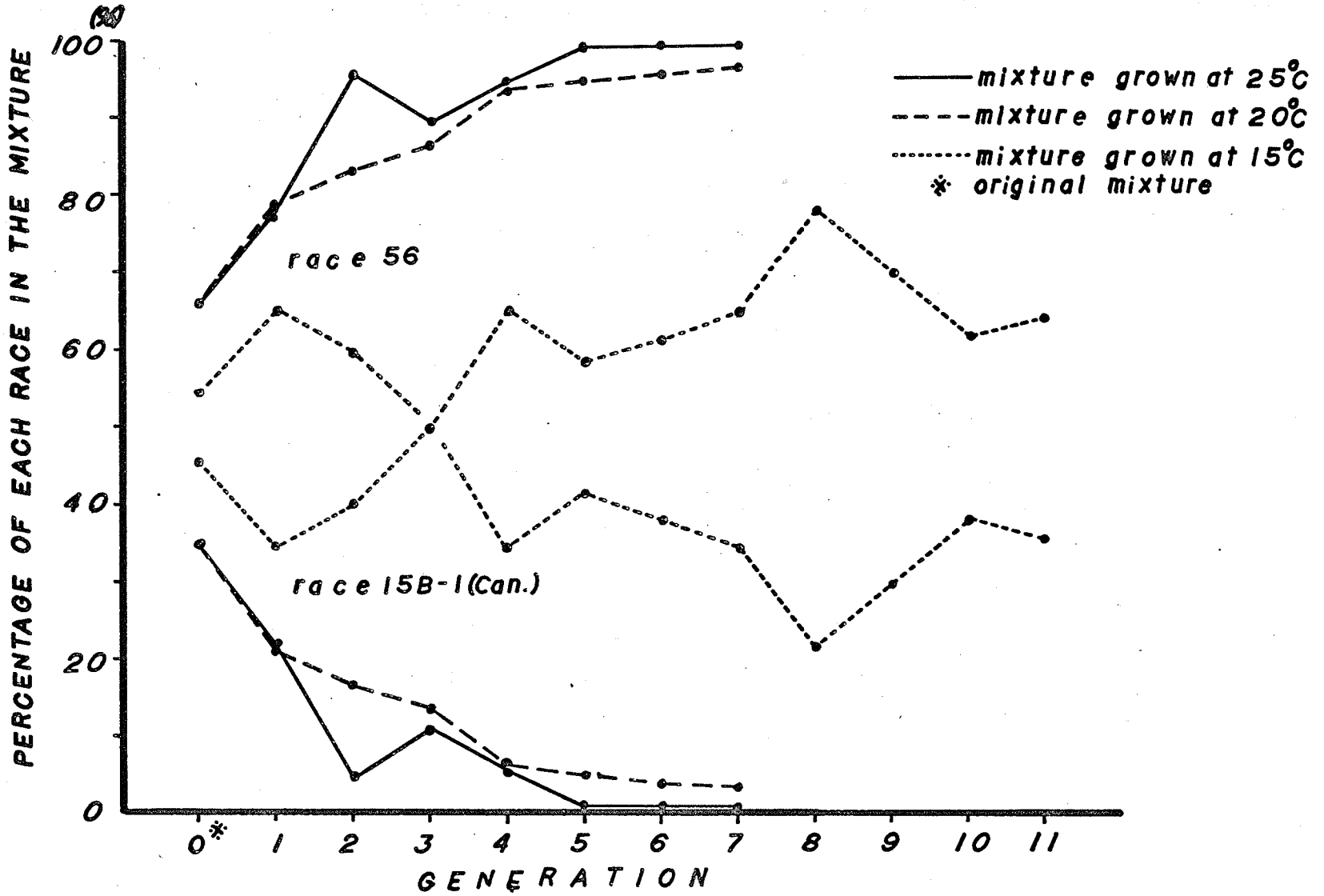


Figure 4. Percentage of survival of races 15B-1 (Can.) and 56 grown in mixtures on the variety Marquis for 11 generations at 15°, 20°, and 25°C.

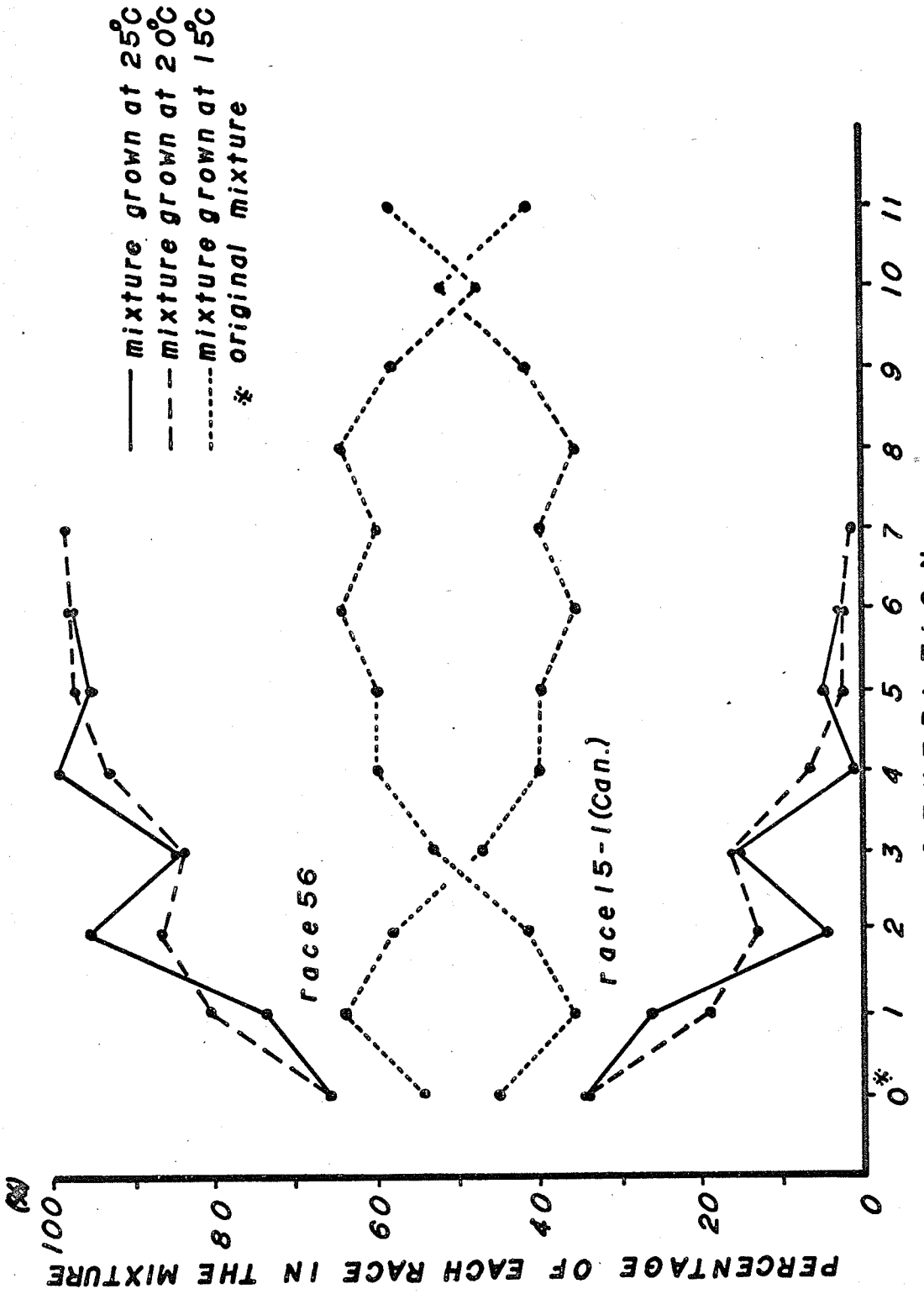


Figure 5. Percentage of survival of races 15B-1 (Can.) and 56 grown in mixtures on the variety Red Bobs for 11 generations at 15°, 20°, and 25°C.

The results on all three host varieties at 15°C were quite different. Race 15B-1 (Can.) predominated over race 56, but not to the same extent as race 56 at the higher temperatures. The experiment was extended over 11 uredial generations on Red Bobs and Marquis but race 56 was not eliminated.

ii) Normal colored races and grayish-brown mutant

The competitive ability of races 15B-1 (Can.) and 56 was then compared at 15° and 20°C on Little Club for 11 generations with the competitive ability of the grayish-brown mutant to check on the accuracy of the above results. The competitive abilities of race 15B-1 (Can.) and the mutant were about equal (Figure 6), but race 56 in mixed infection with the mutant soon predominated at both temperatures (Figure 7). These results support those described above and indicate that race 56 is much superior to race 15B-1 (Can.) in competitive ability, but the relationship is not a simple one. In this experiment, temperature did not have much effect on the survival abilities of the normal and mutant races. The results indicate that under the conditions of these experiments the grayish-brown mutant is almost the same as race 15B-1 (Can.) and much inferior to race 56 in competitive ability.

These results indicate that temperature may be an important factor influencing the prevalence of race 15B-1 (Can.) and race 56 in nature. One would expect race 56 to predominate at higher temperatures (20°- 25°C) and race 15B-1 (Can.) at lower temperatures (15°C). The results also suggest that the host varieties used did not have much

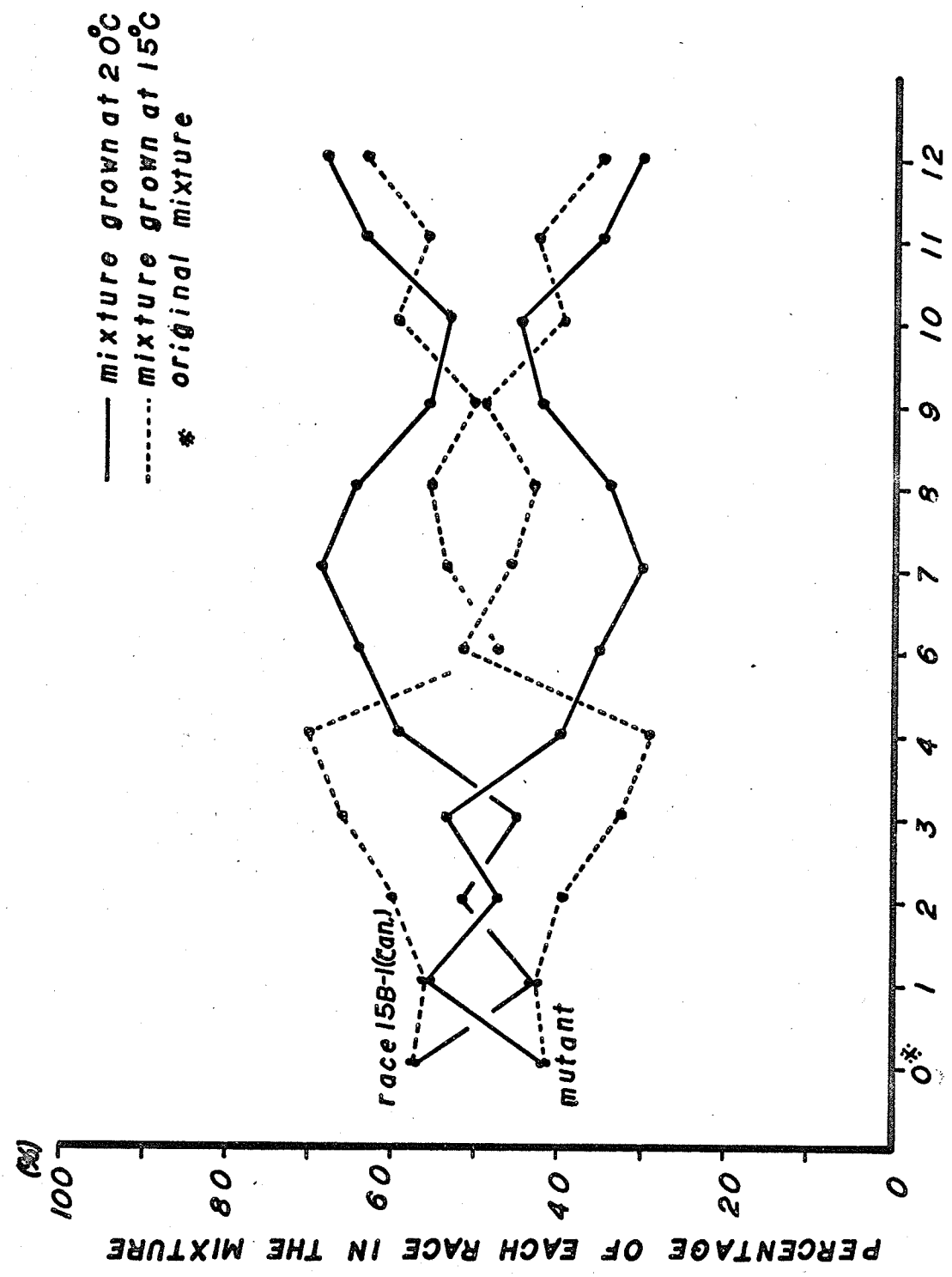


Figure 6. Percentage of survival of races 15B-1 (Can.) and 15 (grayish-brown mutant) grown in mixtures on the variety Little Club for 12 generations at 15° and 20°C.

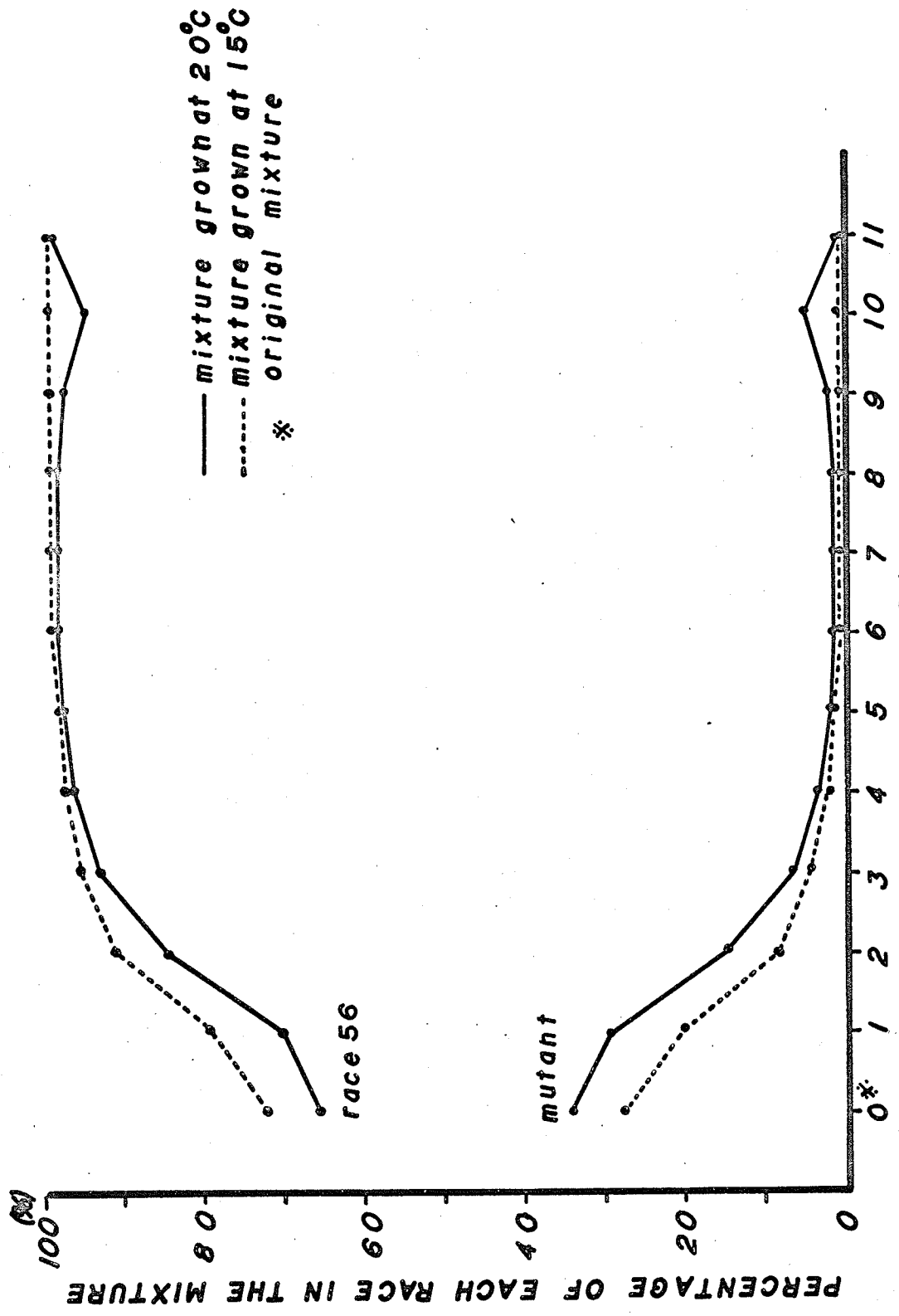


Figure 7. Percentage of survival of races 56 and 15 (grayish-brown mutant) grown in mixtures on the variety Little Club for 11 generations at 15° and 20°C.

influence on the competitive abilities of these races. The study on the competitive ability of normal colored races and the mutant showed no effect of temperature on survival abilities. It seems that temperature may influence the relative prevalence of a race only when certain circumstances exist in the race population.

iii) Relationship between competitive ability and infection density

In the above experiments the predominance of a race may have resulted from faster growth rate or from superior ability to compete for host nutrients. Since these factors might be distinguishable by manipulating infection density, they were investigated by comparing races 15B-1 (Can.) and 56 for competitive ability, rate of pustule growth and incubation period on plants lightly and heavily infected.

The relationship between competitive ability and pustule density was investigated by inoculating seedlings of Little Club and Red Bobs with mixtures of equal amounts of urediospores of races 15B-1 (Can.) and 56 adjusted to produce heavy infections (more than 100 infections per leaf) and light infections (less than 10 infections per leaf). Fourteen uredial generations were studied in duplicate experiments (1 and 2) at both infection densities at 15° and 20°C. In Experiment 1 the mixture at 15°C on heavily infected Little Club became contaminated at the 8th generation and was discarded. After 10 generations on lightly infected plants at 20°C race 15B-1 (Can.) was eliminated. The results of the two experiments were similar and were averaged for presentation in Table 3a and Figures 8a, 8b, 9a,

and 9b. On lightly infected Little Club and Red Bobs race 56 predominated over race 15B-1 (Can.) at 15° and 20°C but on heavily infected Little Club grown at 15° and 20°C race 15B-1 (Can.) became predominant. Similarly on Red Bobs infected heavily at 15°C race 15B-1 (Can.) predominated over race 56, but at 20°C race 15B-1 (Can.) and race 56 were about equal in competitive ability.

When seedlings of Little Club were heavily infected with mixtures of urediospores of races 15B-1 (Can.) or 56 and the grayish-brown mutant and grown at 15° and 20°C, the survival rate of races 15B-1 (Can.) and 56 gradually diminished from the 1st to the 7th uredial generation (Table 3b and Figures 10a and 11a). When the plants were lightly infected the survival rate of the mutant was superior to race 15B-1 (Can.) at 15°C but inferior at 20°C (Figure 10b). In mixed infections with race 56 at 15°C the mutant survived well for the first four generations but then gave way to race 56. At 20°C the survival of the mutant quickly diminished (Figure 11b).

The results of the experiment in which the competitive abilities of races 15B-1 (Can.) and 56 were compared at two levels of infection indicate that race 15B-1 (Can.) is the better competitor when infection is heavy but the poorer competitor when infection is light. The experiment in which the grayish-brown mutant was compared with races 15B-1 (Can.) and 56 provided further information on this point. The reason for the superior competitive ability of race 15B-1 (Can.) when infection was heavy is not clear but could be explained by presuming that race 15B-1 (Can.) is the stronger competitor for

Table 3a. Comparison of the competitive abilities of races 15B-1 (Can.) and 56 on lightly and heavily infected seedlings of the varieties Little Club and Red Bobs.

Generation	Temp. (°C)	Number of infections			
		1) Little Club		Red Bobs	
		Light	Heavy	Light	Heavy
		15B-1 : 56 (Can.)	15B-1 : 56 (Can.)	15B-1 : 56 (Can.)	15B-1 : 56 (Can.)
2) Original Mixture	15	142 : 142	110 : 116	154 : 159	155 : 176
1	"	24 : 69	51 : 20	18 : 44	83 : 83
2	"	7 : 155	159 : 16	76 : 175	73 : 24
3	"	37 : 85	325 : 74	48 : 123	144 : 77
4	"	56 : 88	157 : 38	6 : 44	82 : 30
5	"	137 : 222	149 : 36	41 : 237	63 : 11
6	"	85 : 244	182 : 42	40 : 398	376 : 65
7	"	39 : 75	132 : 26	3 : 36	89 : 15
8	"	138 : 424	50 : 18	18 : 58	51 : 9
9	"	3 : 17	36 : 8	11 : 61	33 : 9
10	"	40 : 221	351 : 190	48 : 377	259 : 105
11	"	17 : 177	201 : 59	3 : 44	133 : 103
12	"	2 : 20	76 : 8	4 : 80	92 : 54
13	"	0 : 230	130 : 31	1 : 33	22 : 55
14	"	1 : 467	565 : 38	2 : 419	82 : 183
2) Original mixture	20	183 : 251	145 : 248	99 : 136	139 : 177
1	"	20 : 79	71 : 100	22 : 43	76 : 90
2	"	51 : 168	114 : 165	136 : 453	108 : 270
3	"	54 : 120	142 : 116	68 : 314	70 : 60
4	"	62 : 186	219 : 194	56 : 146	130 : 134
5	"	58 : 255	262 : 200	13 : 58	219 : 105
6	"	69 : 772	314 : 134	48 : 451	259 : 237
7	"	7 : 184	342 : 268	13 : 320	254 : 203
8	"	5 : 357	211 : 115	2 : 272	123 : 118
9	"	0 : 19	117 : 61	1 : 45	60 : 57
10	"	1 : 236	231 : 109	0 : 222	6 : 11
11	"		136 : 45		217 : 232
12	"		282 : 95		195 : 304
13	"		229 : 67		112 : 206
14	"		132 : 66		206 : 610

1) Heavy: Heavy infection, Light: Light infection

2) Original mixture used in each test was assayed on Mindum at the temperature indicated.

Table 3b. Comparison of the competitive abilities of races 15B-1 (Can.) and 56 and a grayish-brown mutant on lightly and heavily infected plants of the variety Little Club.

Generation	Temp. (°C)	Number of infections			
		Light infection	Heavy infection	Light infection	Heavy infection
		15B-1 : Mutant	15B-1 : Mutant	56 : Mutant	56 : Mutant
Original mixture	15	81 : 35	507 : 469	123 : 108	275 : 503
1	"	203 : 125	553 : 1128	279 : 270	461 : 1143
2	"	103 : 171	267 : 1809	131 : 127	202 : 1801
3	"	70 : 278	86 : 2285	305 : 261	249 : 2370
4	"	255 : 483	90 : 2650	680 : 261	253 : 2510
5	"	130 : 302	74 : 3670	313 : 72	239 : 3620
6	"	221 : 250	22 : 2330	615 : 80	35 : 2180
7	"	334 : 536	42 : 3500	666 : 48	72 : 4200
Original mixture	20	48 : 32	633 : 649	113 : 80	380 : 575
1	"	330 : 82	295 : 715	286 : 169	316 : 946
2	"	327 : 52	278 : 1567	353 : 141	278 : 1614
3	"	134 : 20	347 : 2382	230 : 35	208 : 2820
4	"	674 : 79	95 : 2000	588 : 67	218 : 2100
5	"	506 : 45	65 : 2920	547 : 52	206 : 2500
6	"	534 : 70	17 : 2590	826 : 17	388 : 3650
7	"	317 : 6	319 : 2970	177 : 3	76 : 3080

host nutrients when the requirement for them is greatest. Race 56, on the other hand, is the better competitor when infection is light and stress on the nutrient supply is lowest, presumably because it grows more rapidly than race 15B-1 (Can.). The results of the second experiment (Table 3b) suggest that these competitive relationships may be influenced by temperature. On lightly infected plants race 15B-1 (Can.) was a better competitor at 20°C than at 15°C.

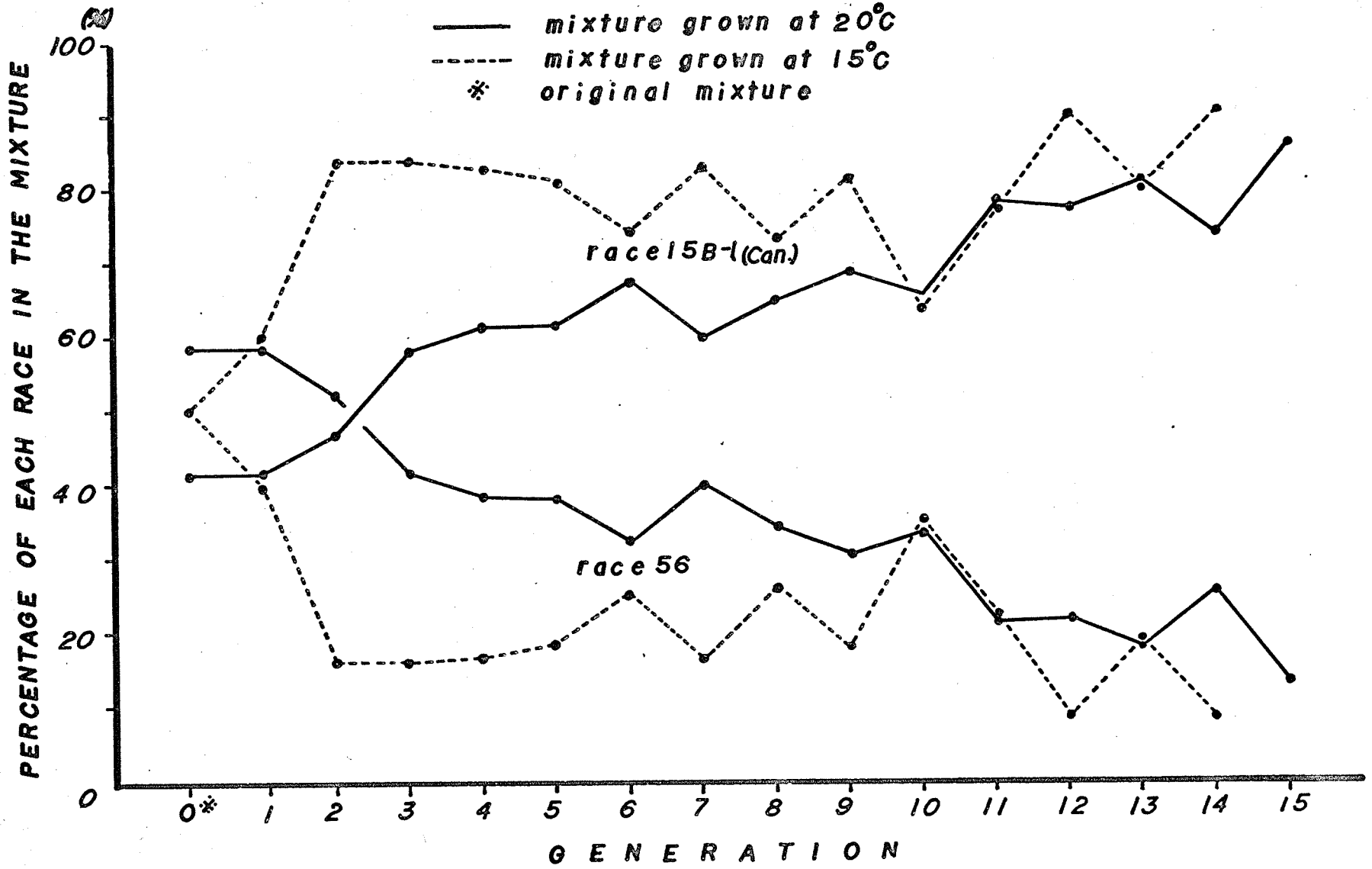


Figure 8a. Comparison of the competitive abilities of races 15B-1 (Can.) and 56 grown on heavily infected seedlings of the variety Little Club for 15 generations at 15° and 20°C.

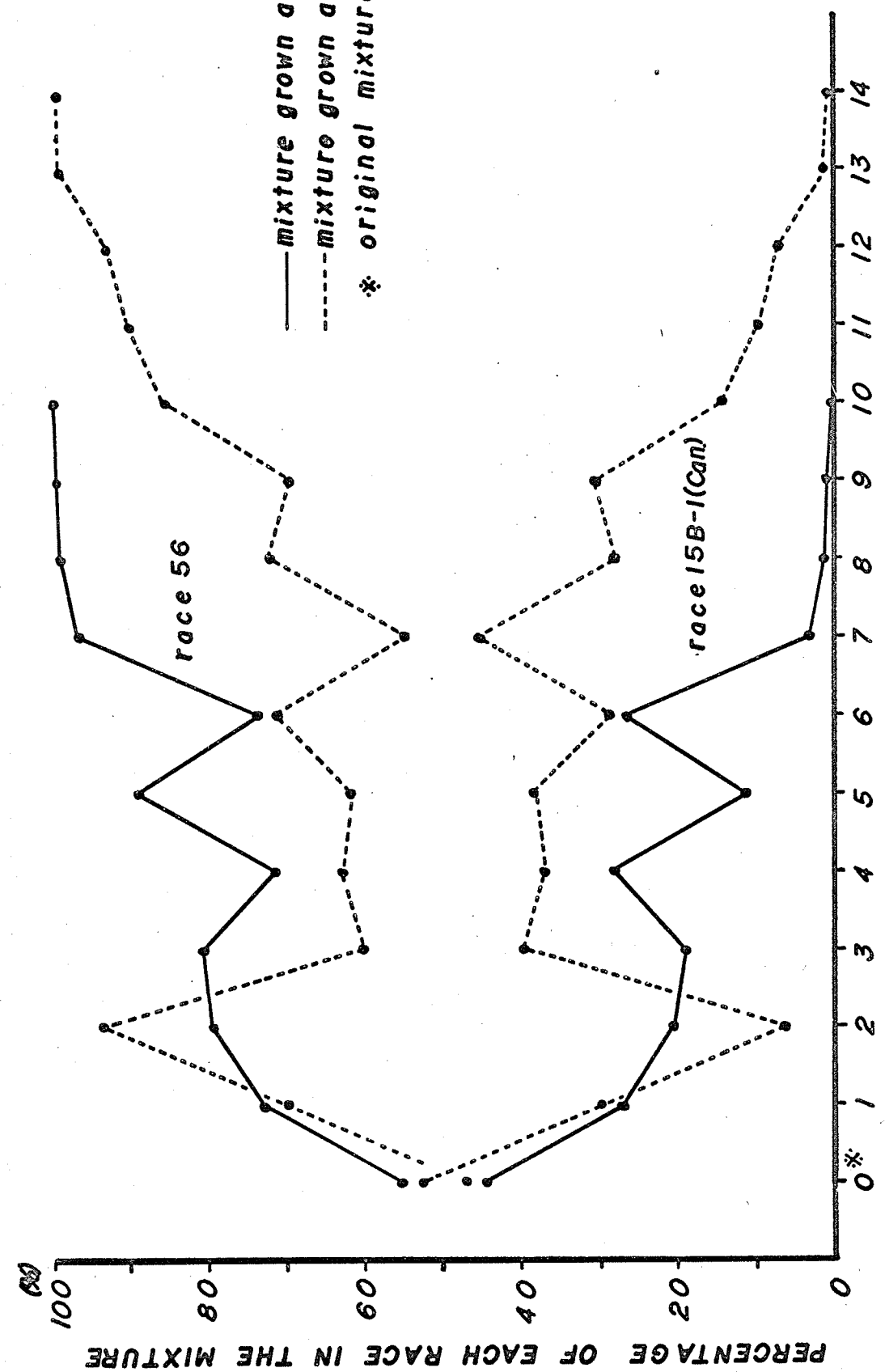


Figure 8b. Comparison of the competitive abilities of races 15B-1 (Can.) and 56 grown on lightly infected seedlings of the variety Little Club for 14 generations at 15° and 20°C.

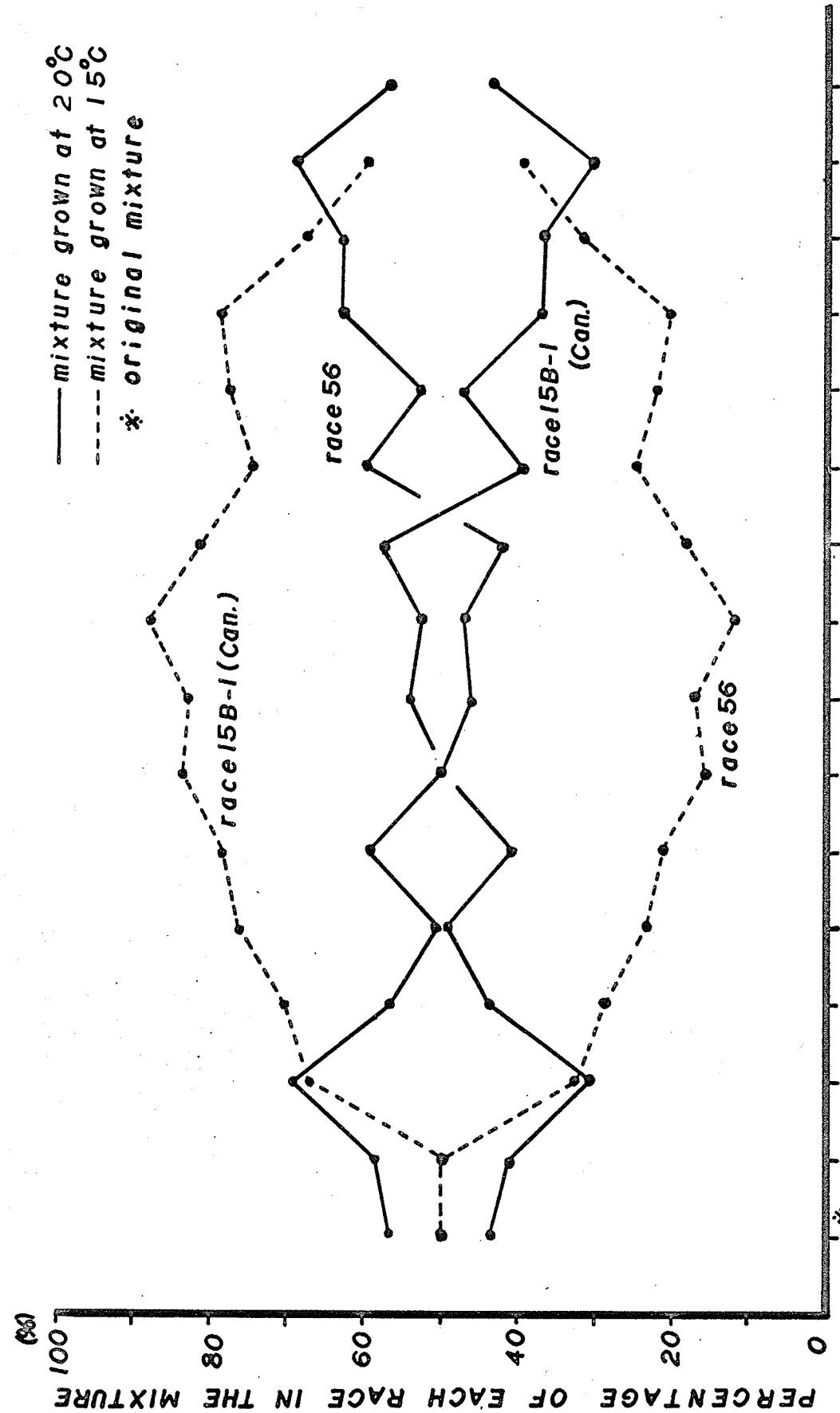


Figure 9a. Comparison of the competitive abilities of races 15B-1 (Can.) and 56 grown on heavily infected seedlings of the variety Red Bobs for 15 generations at 15° and 20°C.

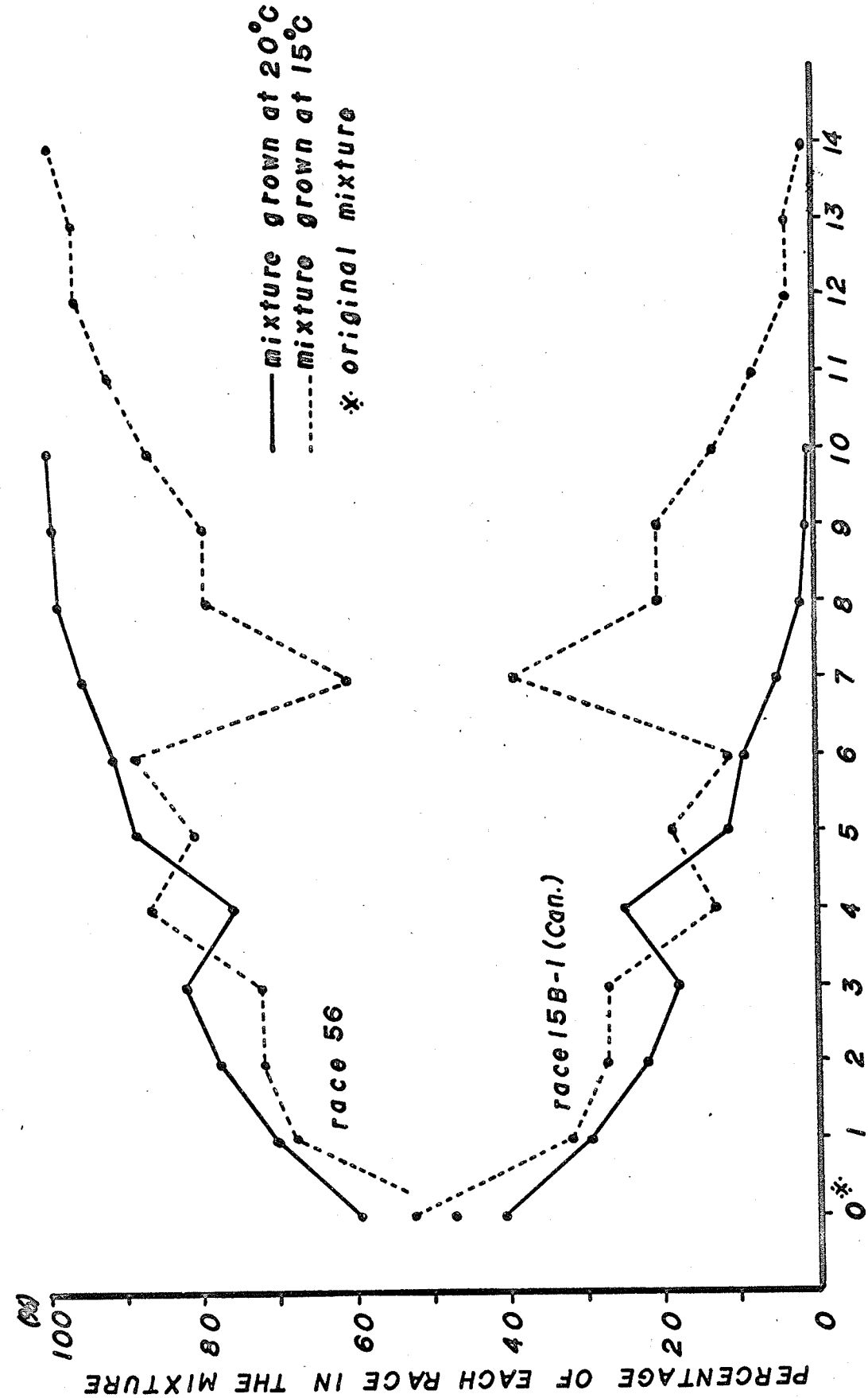


Figure 9b. Comparison of the competitive abilities of races 15B-1 (Can.) and 56 grown on lightly infected seedlings of the variety Red Bobs for 14 generations at 15° and 20°C.

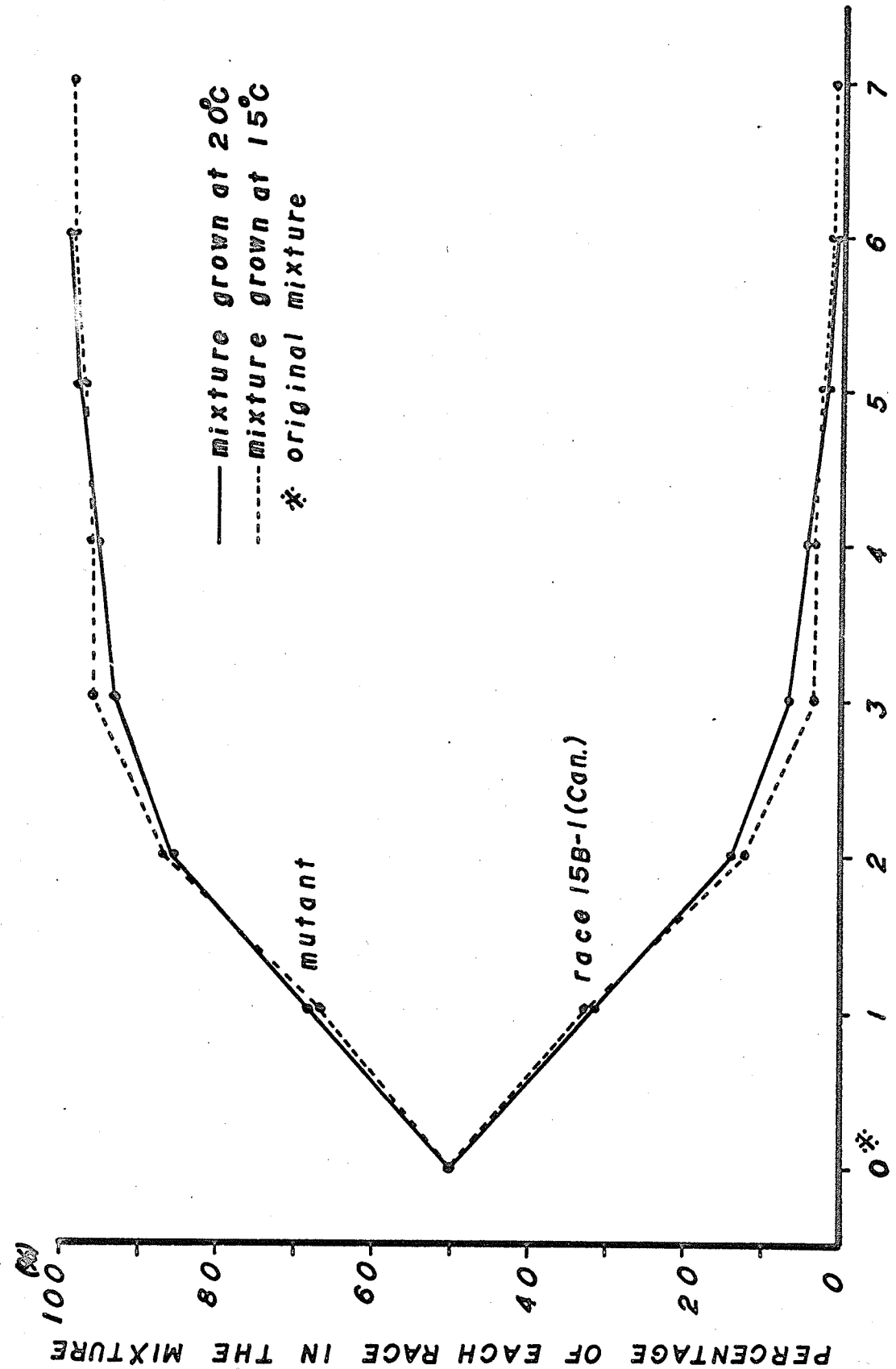


Figure 10a. Comparison of the competitive abilities of races 15B-1 (Can.) and 15 (grayish-brown mutant) grown on heavily infected seedlings of the variety Little Club for 7 generations at 15° and 20°C.

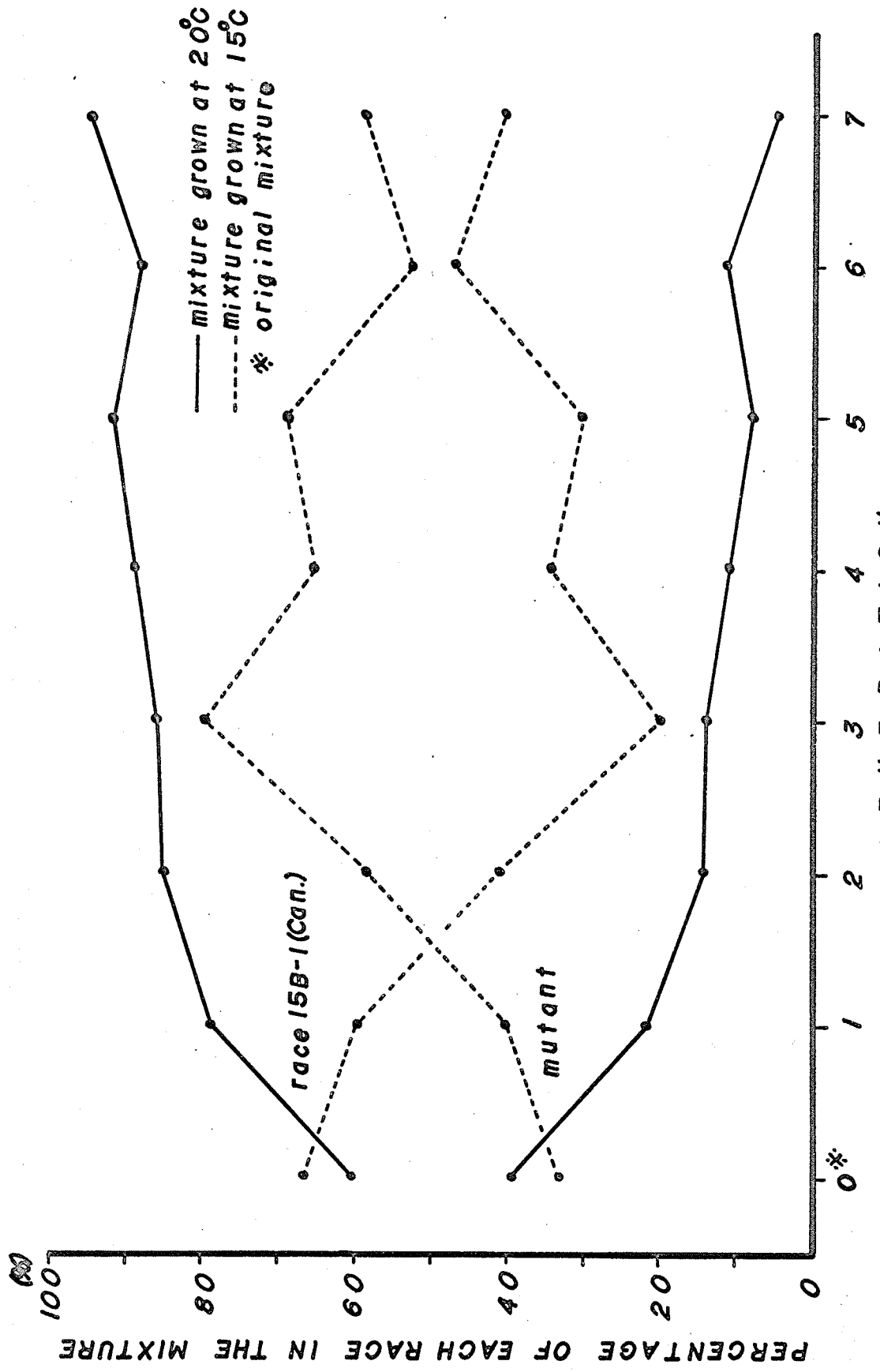


Figure 10b. Comparison of the competitive abilities of races 15B-1 (Can.) and 15 (grayish-brown mutant) grown on lightly infected seedlings of the variety Little Club for 7 generations at 15° and 20°C.

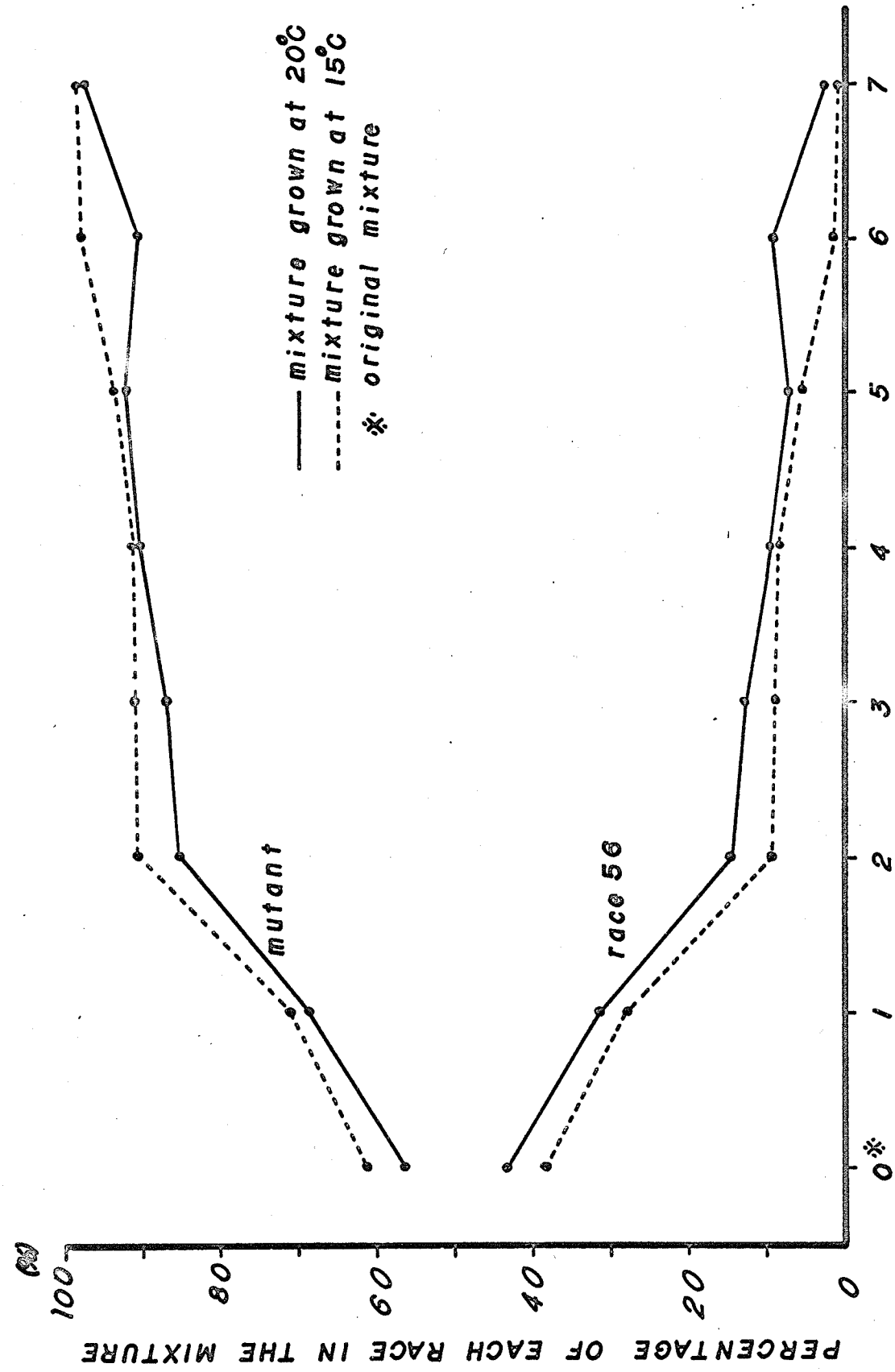


Figure 11a. Comparison of the competitive abilities of races 56 and 15 (grayish-brown mutant) grown on heavily infected seedlings of the variety Little Club for 7 generations at 15^{0} and 20^{0}C.

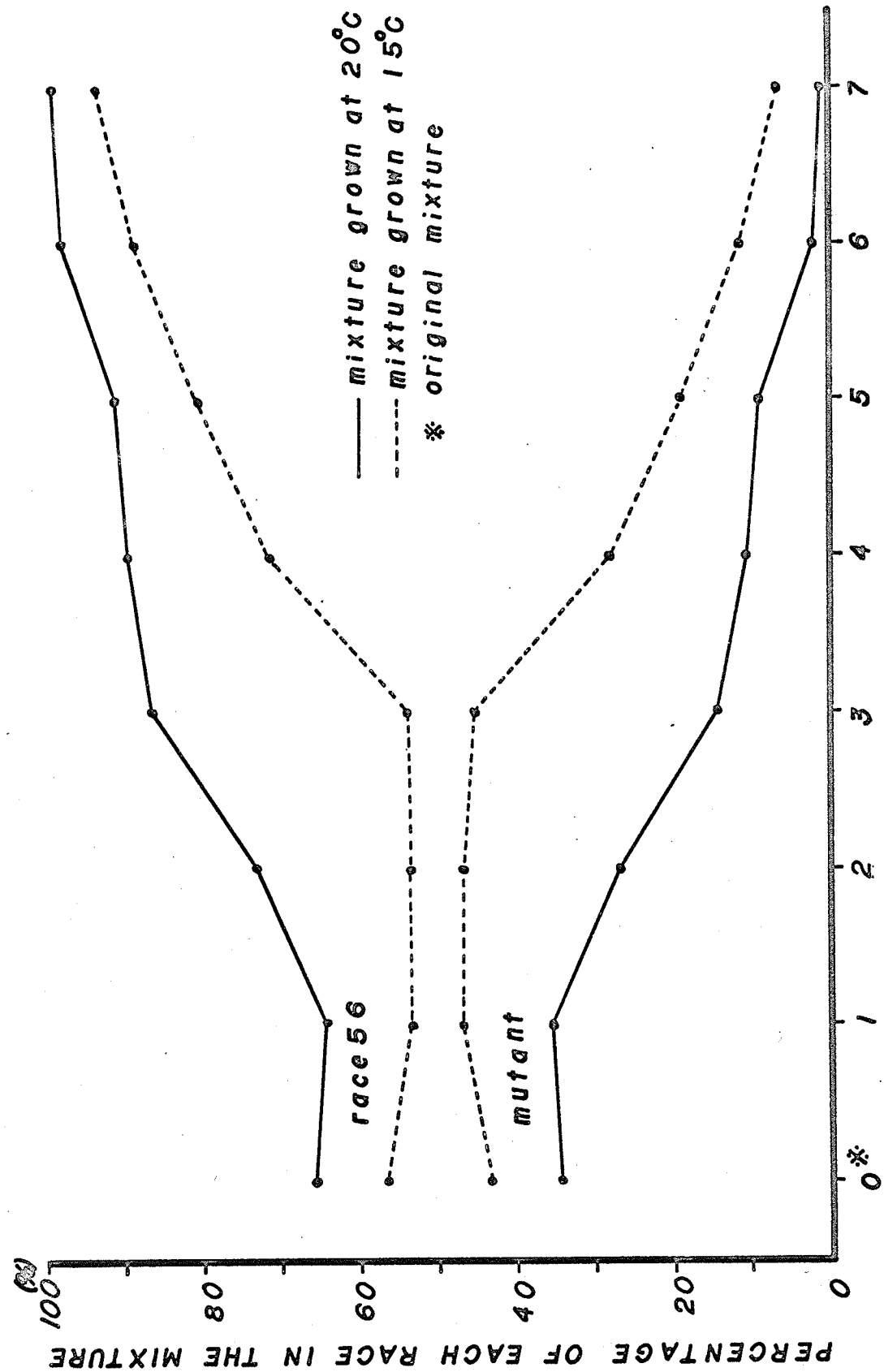


Figure 11b. Comparison of the competitive abilities of races 56 and 15 (grayish-brown mutant) grown on lightly infected seedlings of the variety Little Club for 7 generations at 15° and 20°C.

Spore Viability

i) Germinability

The viability of the urediospores produced by races 15B-1 (Can.) and 56 was investigated first by determining their germinability. Fresh urediospores of single spore cultures of each race were seeded on 1% water agar and incubated at room temperature. The germination rates of three single spore cultures of race 15B-1 (Can.) were slightly higher than those of race 56 (Table 4).

Table 4. Germination of urediospores of single spore cultures of races 15B-1 (Can.) and 56 of wheat stem rust at room temperature.

Race	Single spore isolate No.	Total spores counted	Percentage of germination
15B-1 (Can.)	II	1200	94.7
15B-1 (Can.)	X	1200	90.6
15B-1 (Can.)	XI	1200	91.0
56	IV	800	87.6
56	XI	800	84.6
56	XIII	782	85.7

Differences between single spore cultures of the same race were not statistically significant at the 5% level, but the difference between races was significant at the 5% level. At temperatures of 5° to 35°C the germination rates of urediospores of a single spore culture of race 15B-1 (Can.) were slightly higher than those of a single spore culture of race 56 (Table 5). When the urediospores of each were seeded on the wet under-surface of wheat leaves in moist

petri dishes for germination, the germination rate of both races was not very different (Table 6). It was frequently observed that at about two hours after seeding the spores on 1% water agar, germination of race 15B-1 (Can.) was slightly faster than that of race 56 (at temperature of 20°C, 1.8% for race 15B-1 (Can.) and 0.7% for race 56).

Table 5. Germination of urediospores of races 15B-1 (Can.) and 56 of wheat stem rust at seven temperatures.

Race	Temperature (°C)	Total spores counted	Percentage of germination
15B-1 (Can.)	5	900	30.6
56	"	900	28.9
15B-1 (Can.)	10	900	67.2
56	"	900	67.9
15B-1 (Can.)	15	900	70.6
56	"	900	60.0
15B-1 (Can.)	20	900	79.0
56	"	900	76.9
15B-1 (Can.)	25	900	75.7
56	"	900	70.6
15B-1 (Can.)	30	900	71.2
56	"	900	56.7
15B-1 (Can.)	35	900	0.0
56	"	900	0.0

The results from tests on spore germinability indicate that race 15B-1 (Can.) is slightly superior to race 56 on water agar but almost the same on wheat leaves. The germinabilities of races 15B-1 (Can.) and 56 may not be different in nature. However, if the

Table 6. Germination of urediospores of races 15B-1 (Can.) and 56 on the leaves of four varieties of wheat at three temperatures.

Race	Variety	Percentage of germination		
		15°C	20°C	25°C
15B-1 (Can.)	Little Club	88.6	83.5	88.7
56	"	83.5	85.7	90.7
15B-1 (Can.)	Red Bobs	88.7	86.7	93.5
56	"	89.3	90.4	94.3
15B-1 (Can.)	Marquis	88.2	89.3	93.1
	"	86.8	86.2	90.0
15B-1 (Can.)	Mindum	88.8	87.0	76.0
56	"	87.5	58.7	76.5

urediospores of race 15B-1 (Can.) germinate faster than those of race 56 on the wheat leaves, race 15B-1 (Can.) may have an advantage in infecting the host plants.

ii) Spore-longevity

Fresh urediospores of races 15B-1 (Can.) and 56 were kept separately in petri dishes in growth chambers at 15°, 20°, and 25°C. The experiment was done in duplicate. The results are shown in Figures 12a and 12b. The germinability of the spores of both races kept at 25°C was not much changed after 4 days of storage but afterwards it reduced quickly. Eighteen days later the germination rate of both races kept at 25°C was about 1%. The spores of race 15B-1 (Can.) kept at 25°C germinated slightly better than those of race 56 during the first 16 days of storage. The longevity of spores of both races diminished at about the same rate when the spores were stored at

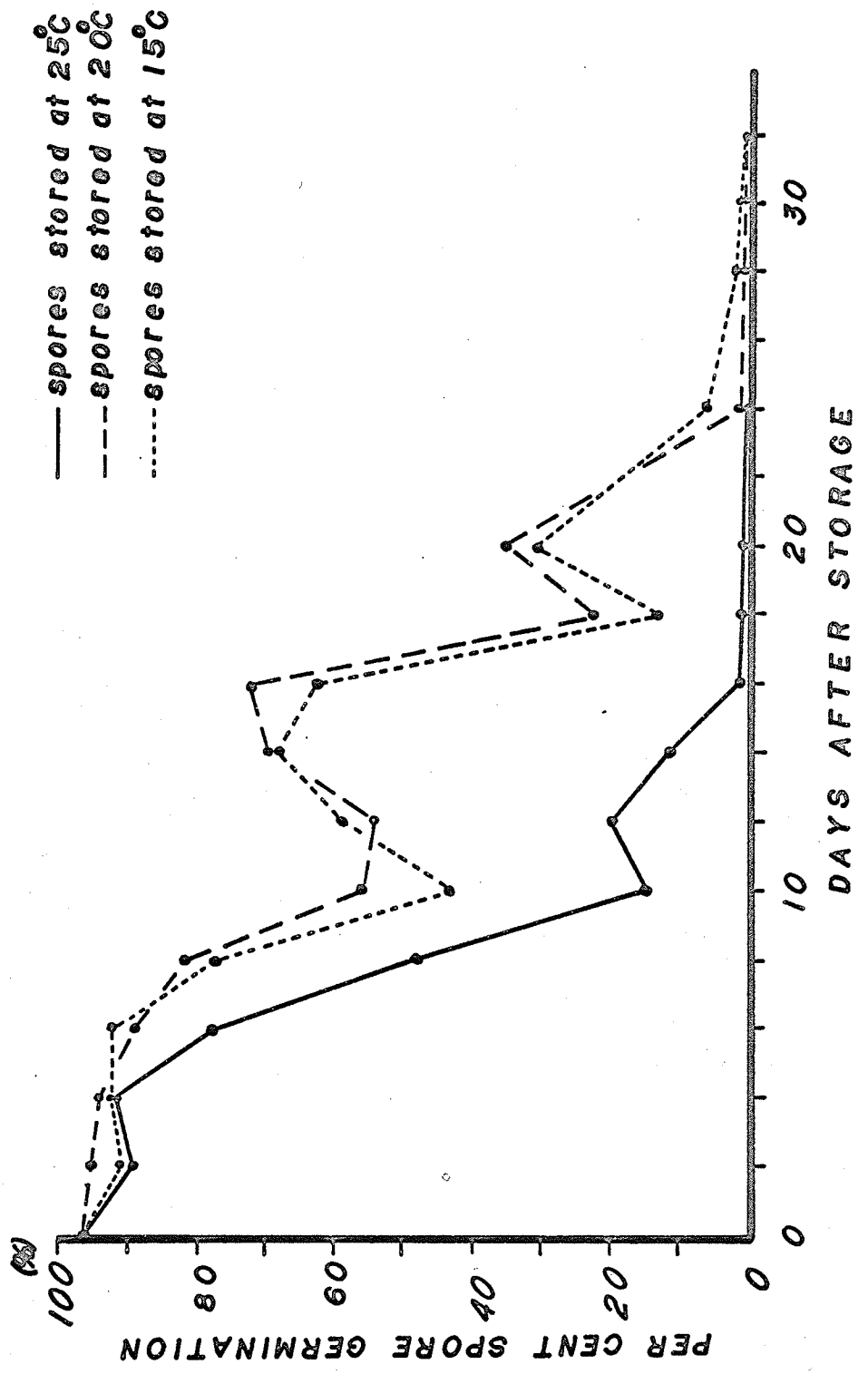


Figure 12a. Per cent germination of urediospores of race 15B-1 (Can.) after storage at 15°, 20°, and 25°C.

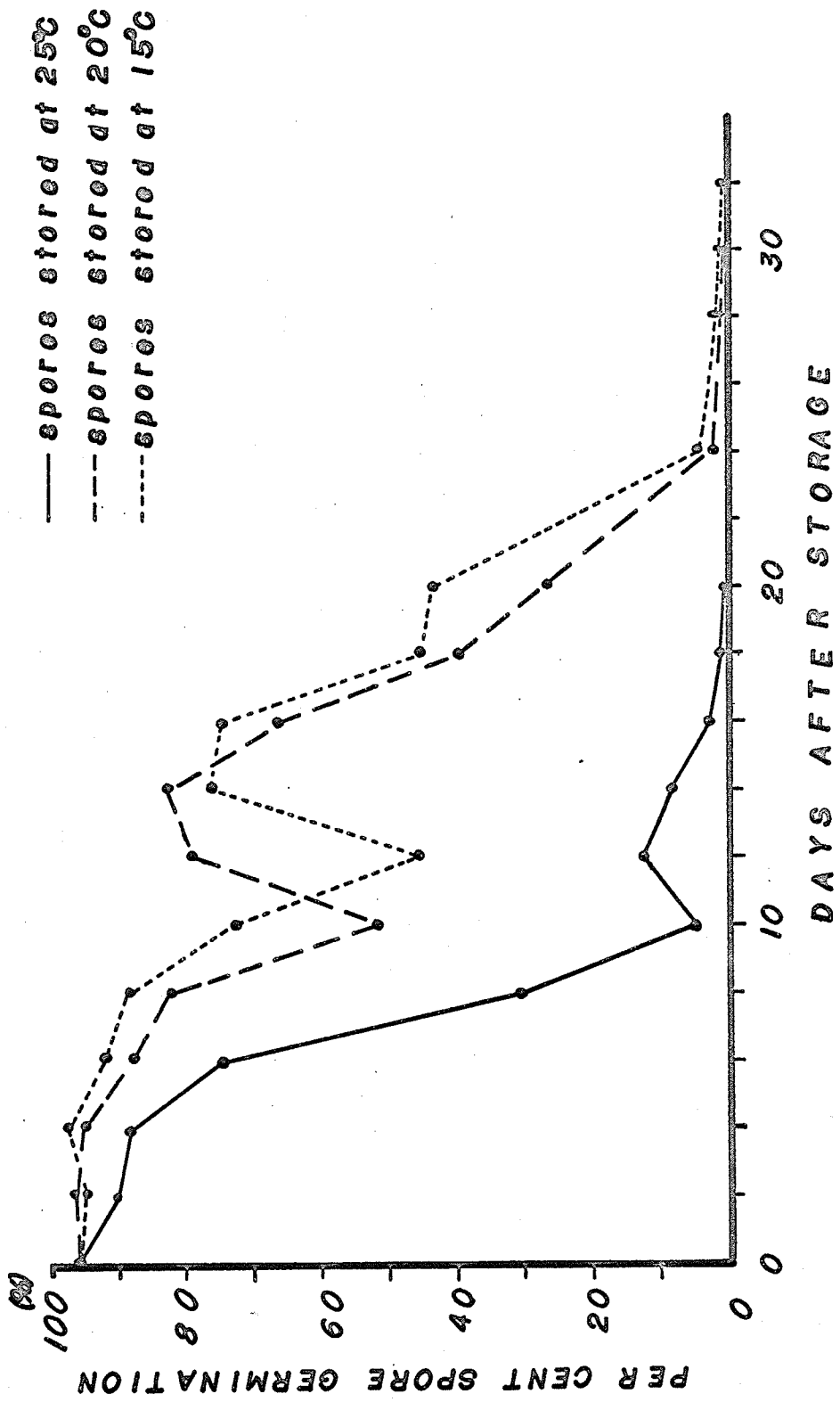


Figure 12b. Per cent germination of urediospores of race 56 after storage at 15°, 20°, and 25°C.

15° and 20°C. However, the spores of race 56 kept at 15°C germinated a little better than those of race 15B-1 (Can.).

Two mgs of fresh urediospores were vacuum-sealed in glass tubes and the sealed tubes were kept in the growth chambers at 15°, 20°, and 25°C. The germination of the spore samples was tested on 1% water agar after 0, 7, and 42 days of storage. The results given in Table 7, show that there was no significant difference in loss of viability between the two races.

Table 7. Longevity of urediospores of races 15B-1 (Can.) and 56 stored in evacuated tubes at three temperatures.

Days after collection	Percentage of germination					
	Race 15B-1 (Can.)			Race 56		
	15°C	20°C	25°C	15°C	20°C	25°C
0 (Check)*	28.8	28.8	28.8	25.0	25.0	25.0
7	23.0	20.4	20.8	33.0	20.8	18.4
42	7.6	3.6	1.6	2.0	1.0	2.0

* Tubes examined immediately after evacuation and before storage at the various temperatures.

These results on spore-longevity indicate that at high temperature (25°C) the spores quickly lose their viability but at moderate and low temperatures (15° - 20°C) the loss of viability is less but both races show a similar tendency.

Infective Ability

In the experiments on single spore infection, the rate of infection on Little Club seedlings was the same (2.3%) for races 15B-1 (Can.) and 56. Further tests on the infectivity of races 15B-1 (Can.) and 56 were made by spraying suspensions with definite

amounts (11 or 20 mgs) of fresh urediospores on wheat seedlings grown at 15°, 20°, and 25°C and counting the number of infections on the plants. The infections of race 56 on the wheat varieties Little Club, Red Bobs, and Marquis were usually more numerous than those of race 15B-1 (Can.) (Tables 8a and 8b). The number of infections on the seedlings were different in the wheat varieties tested. Marquis seedlings were usually more readily infected by both races than Red Bobs or Little Club. The influence of temperature on infection was inconsistent in the first experiment (Table 8a) but data from the second experiment (Table 8b) indicate that 20°C is more favorable for infection than 15° or 25°C.

Growth of Pustules

i) Size of pustules

The pustule size (sporulating area) on Little Club leaves infected lightly with each race singly and grown at 15°, 20°, and 25°C was measured with a microscope 8, 10, and 11 days after inoculation. The size of each pustule was calculated from its longitudinal and lateral dimensions. The results given in Table 9 show that the average size of pustules of race 56 grown at all temperatures was larger than that of race 15B-1 (Can.) 8, 10, and 11 days after inoculation. The pustule growth of both races was fastest at 25°C and slowest at 15°C. In experiment 1, pustules of race 56 were about twice the size of those of race 15B-1 (Can.) at 15°C 8 and 10

Table 8a. The infective ability of races 15B-1 (Can.) and 56. (Inoculum: 20 mgs/50 cc)

Expt.	Race	1) Host	Temp. (°C)	Total No. of plants used	Total No. of pustules	Average No. of pustules per leaf
I	15B-1	LC	15	131	1978	15.1
	56	LC	15	129	2164	16.8
	15B-1	RB	15	93	338	3.6
	56	RB	15	86	748	8.5
	15B-1	MA	15	64	843	13.2
	56	MA	15	48	1286	26.8
	15B-1	LC	20	135	1796	13.3
	56	LC	20	127	1513	11.9
	15B-1	RB	20	97	619	6.4
	56	RB	20	83	1402	16.9
	15B-1	MA	20	61	1351	22.1
	56	MA	20	51	1660	32.5
	15B-1	LC	25	92	798	8.7
	56	LC	25	116	1612	13.9
	15B-1	RB	25	69	412	6.1
	56	RB	25	87	867	10.0
	15B-1	MA	25	70	732	10.5
	56	MA	25	47	612	13.0
II	15B-1	LC	20	43	876	20.4
	56	LC	20	30	1003	33.4
	15B-1	RB	20	21	277	13.2
	56	RB	20	24	577	24.0
	15B-1	MA	20	13	139	10.7
	56	MA	20	20	816	40.8
	15B-1	MD	20	20	112	5.6
	56	MD	20	19	131	6.9

1) LC: Little Club, RB: Red Bobs, MA: Marquis, MD: Mindum.

Table 8b. The infective ability of races 15B-1 (Can.) and 56 (Inoculum: 11 mgs/50 cc)

Race	Host	Temp. (°C)	Total No. of plants used	Total No. of pustules	Average No. of pustules per leaf
15B-1	LC	15	58	13	0.2
56	LC	15	70	14	0.2
15B-1	RB	15	28	112	4.0
56	RB	15	29	176	6.1
15B-1	MA	15	27	294	10.9
56	MA	15	29	303	10.4
15B-1	LC	20	62	140	2.3
56	LC	20	57	367	6.4
15B-1	RB	20	26	165	6.3
56	RB	20	24	288	12.0
15B-1	MA	20	30	445	14.8
56	MA	20	32	660	20.6
15B-1	LC	25	52	123	2.4
56	LC	25	59	231	3.9
15B-1	RB	25	27	142	5.3
56	RB	25	26	302	11.6
15B-1	MA	25	38	217	5.7
56	MA	25	38	250	6.6

Table 9. The average size of uredia on rust-infected Little Club leaves.

Expt.	Race	Temp. (°C)	Days after inoculation	No. of plants used	Total No. of uredia	Average size of uredia (mm^2)
	15B-1	15	8	40	75	0.05
	56	15	8	50	207	0.11
	15B-1	20	8	50	184	0.19
	56	20	8	50	192	0.40
I	15B-1	15	10	50	190	0.50
	56	15	10	50	210	1.09
	15B-1	20	10	50	212	2.07
	56	20	10	50	190	2.34
	15B-1	20	8	20	497	0.79
	56	20	8	20	376	1.06
	15B-1	25	8	20	354	0.68
	56	25	8	20	203	1.37
II	15B-1	20	11	17	235	8.67
	56	20	11	20	192	8.86
	15B-1	25	11	17	110	10.96
	56	25	11	19	108	17.41

days after inoculation. At 20°C race 56 also had larger pustules at 8 days but at 10 days the average size of pustules of race 15B-1 (Can.) approached that of race 56. In experiment 2, at 20°C the pustule size of race 56, 11 days after inoculation, showed the same tendency in the experiment 1. The results indicate that pustules of both races grow faster at higher temperatures than at low temperature, and that pustules of race 56 grow faster than those of race 15B-1 (Can.), especially in early stages of development.

ii) Growth rate of pustules

Two methods were used to investigate growth rate of pustules. One was a photographic method by which particular pustules were photographed on every other day and the photographs enlarged to a uniform magnification. The pustules were then measured by means of a planimeter. Pustules on the plants grown at higher temperature could unfortunately not be measured in this way in later stages of growth because the plants were killed by root rot. The second method was by measuring particular pustules with a microscope equipped with an ocular micrometer. The results from the photographic method appear in Figure 13. These show the average size of 5 pustules in each race. Figures 14, 15, and 16, based on microscopic measurement, show growth of individual pustules and the average of 5 pustules of races 15B-1 (Can.) and 56 at 15° and 20°C. Five pustules of each race were measured. These results show that the pustules of race 56 grew faster at early stages of rust development but at later stages pustules of race 15B-1 (Can.) became larger. The time

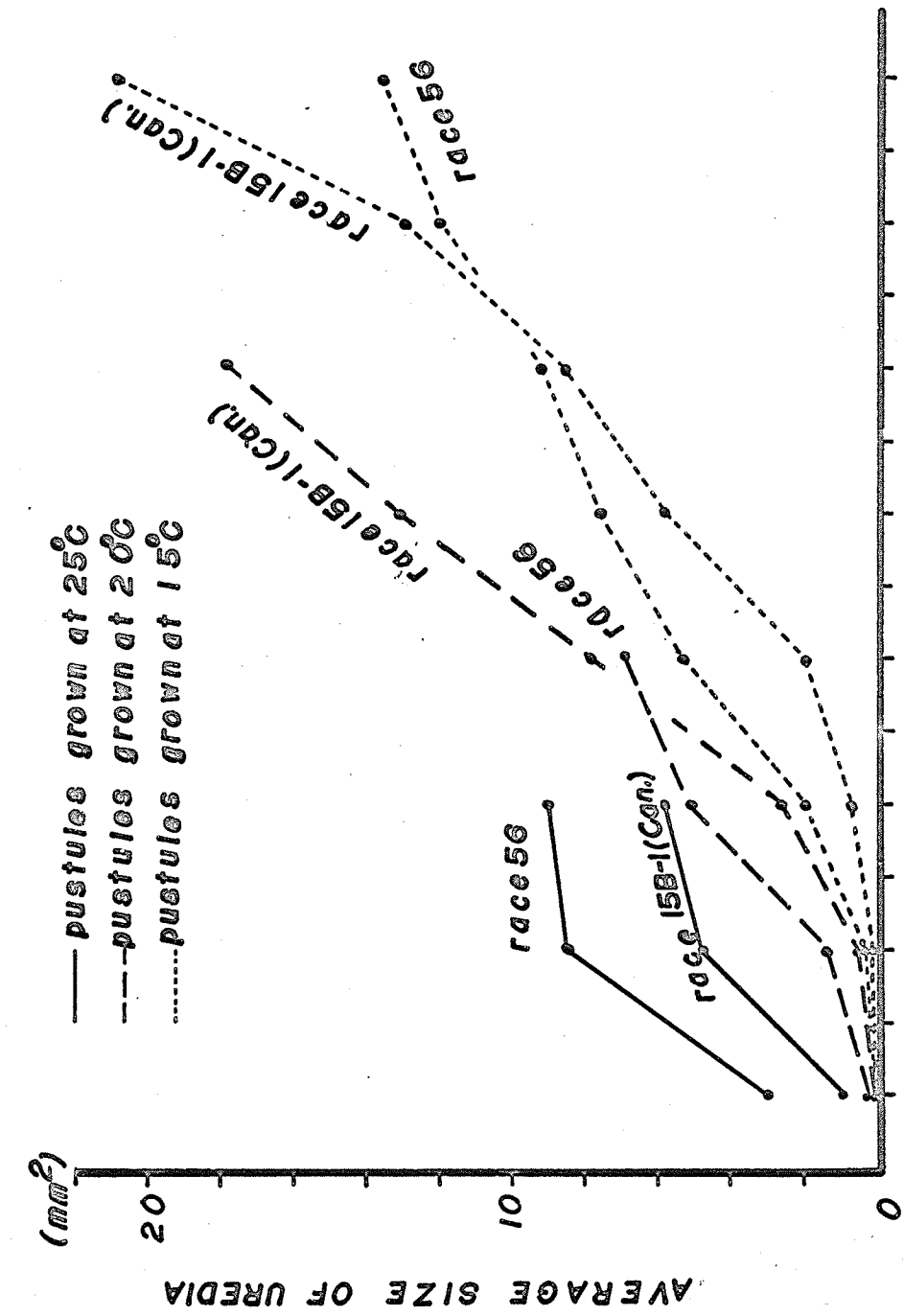


Figure 13. Average growth of five pustules of races 15B-1 (Can.) and 56 grown at 15°, 20°, and 25°C as measured at two-day intervals by a photographic method.

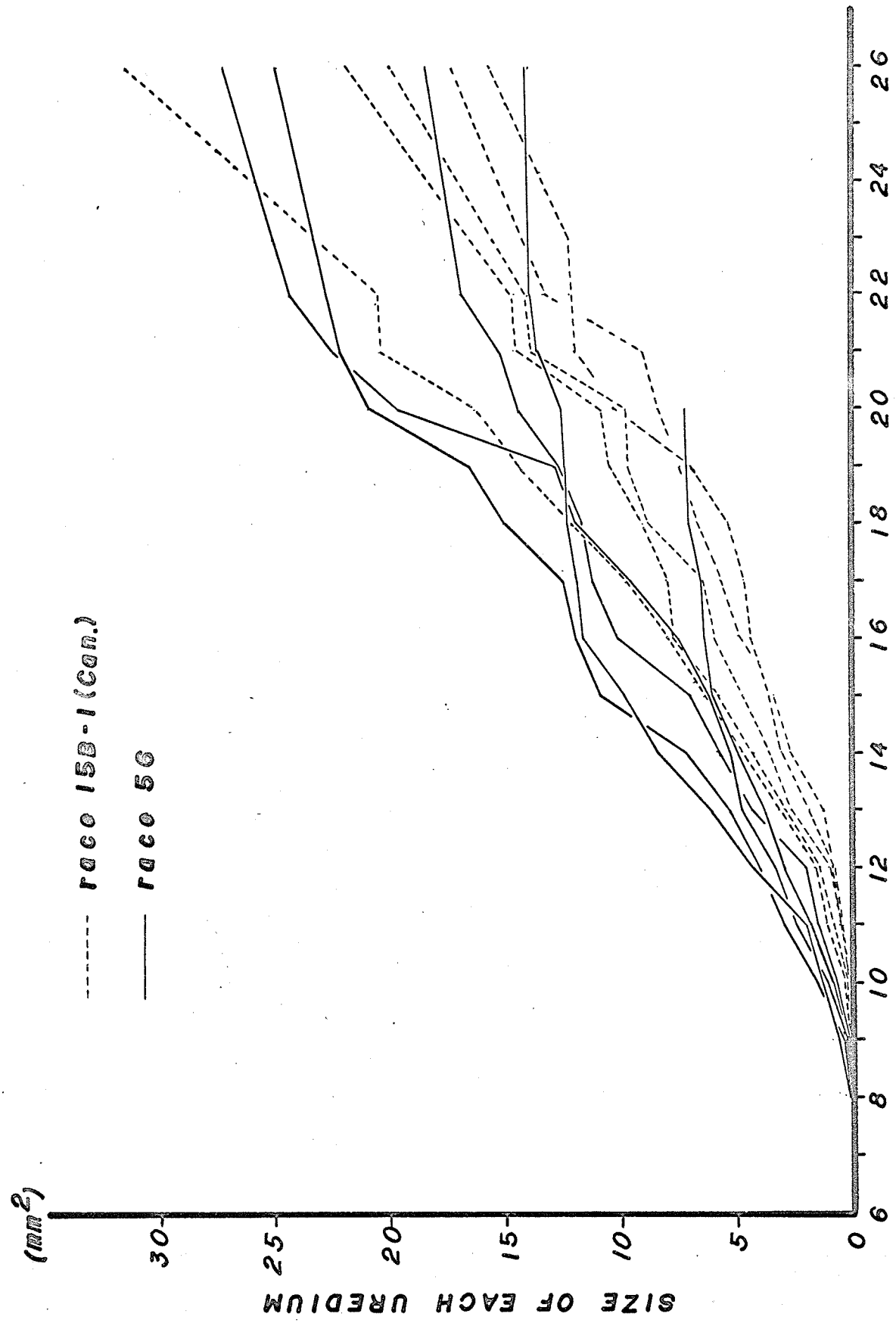


Figure 14. Growth of individual pustules of races 15B-1 (Can.) and 56 grown at 15°C for 26 days after inoculation as measured by a microscopic method.

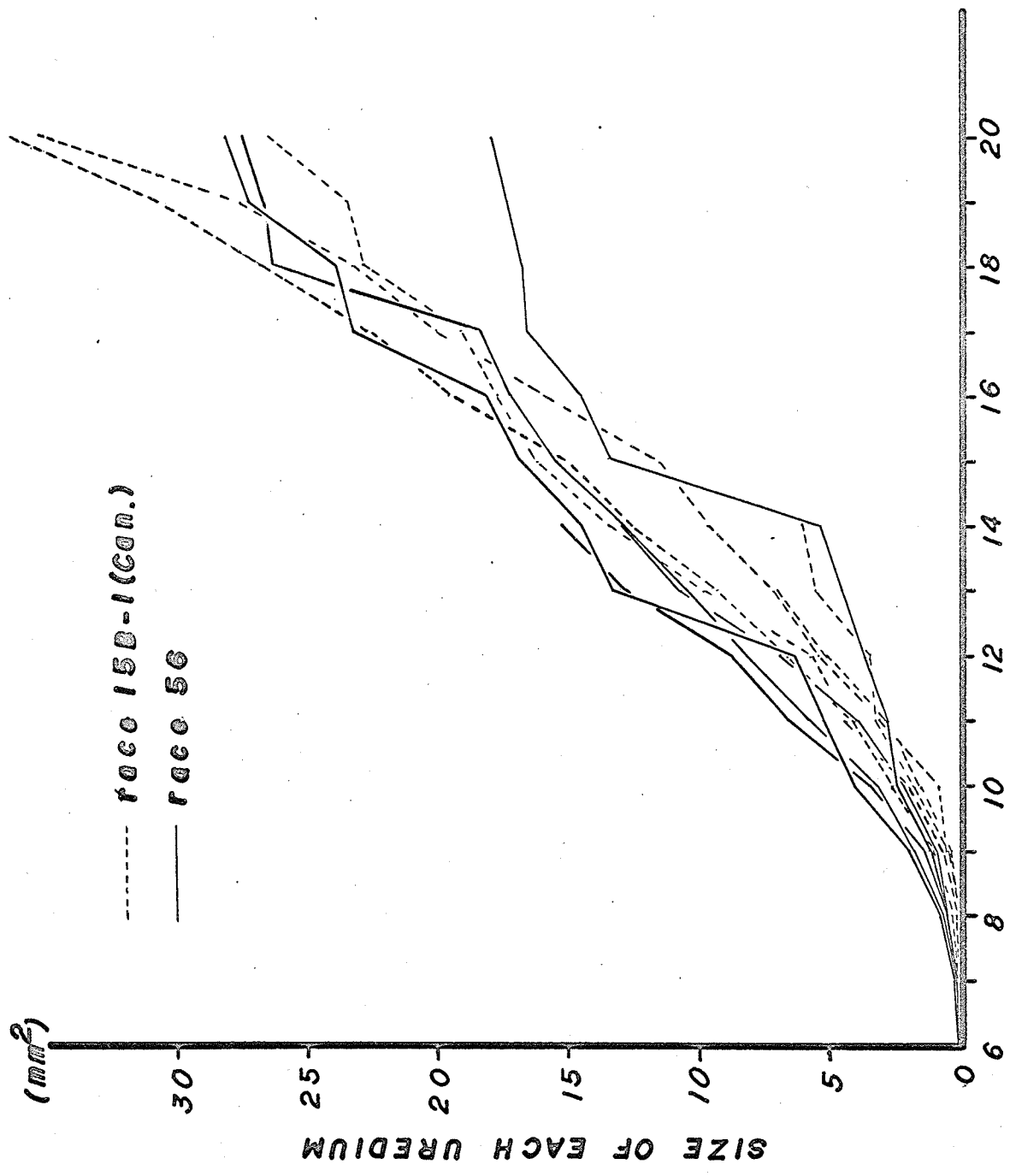


Figure 15. Growth of individual pustules of races 15B-1 (Can.) and 56 grown at 20°C for 20 days after inoculation as measured by a microscopic method.

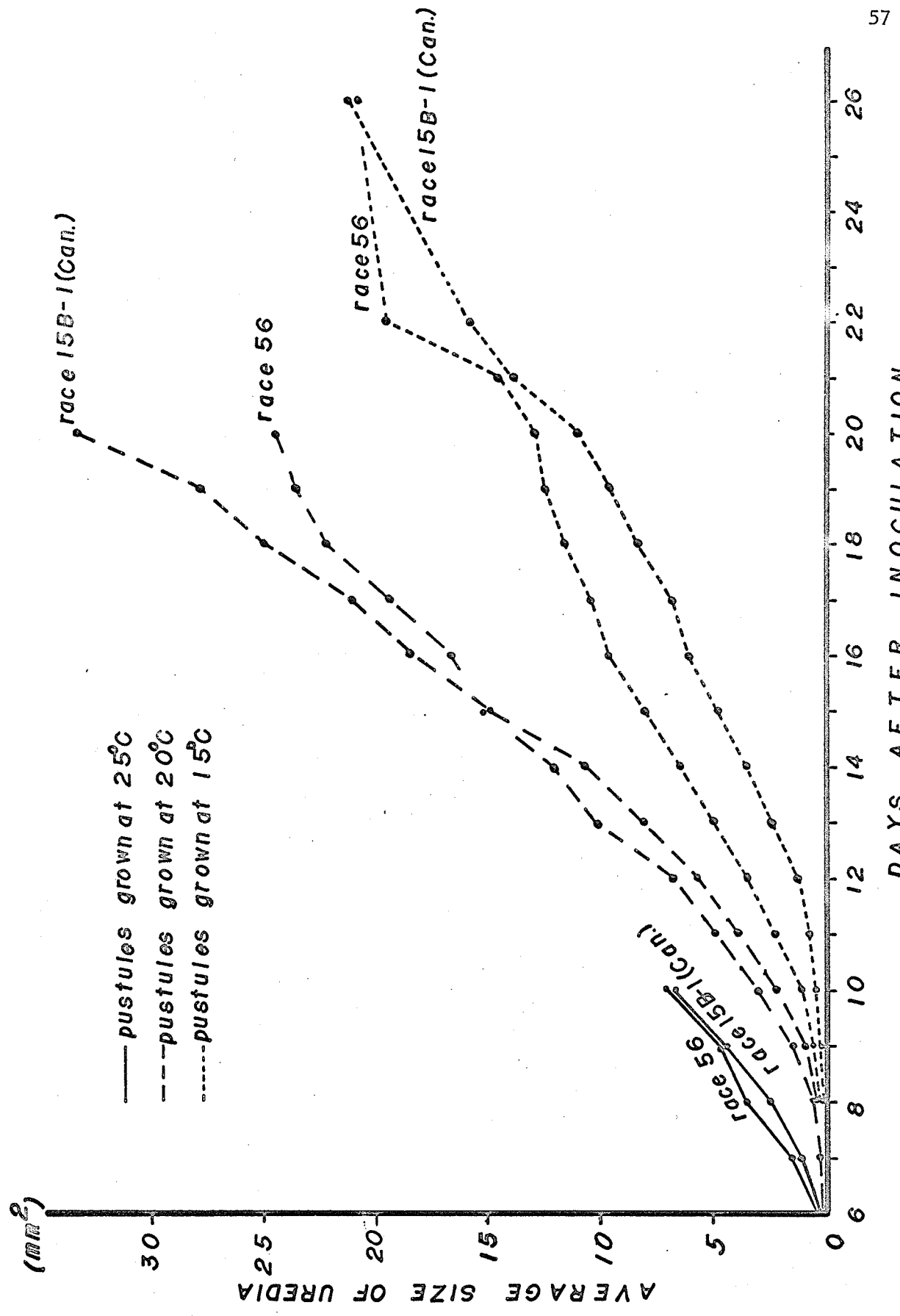


Figure 16. Average growth of five pustules of races 15B-1 (Can.) and 56 grown at 15°, 20°, and 25°C as measured by a microscopic method.

required for pustules of race 15B-1 (Can.) to exceed those of race 56 in size depended on the temperature at which the pustules grew. According to the results from microscopic measurement, the pustules of race 15B-1 (Can.) grown at 25°C may become as large as those of race 56 about 10 days after inoculation, at 20°C about 15 days after inoculation, and at 15°C 26 days after inoculation (Figure 16). In the data from photographic measurement, the pustules of race 15B-1 (Can.) grown at 15°C became larger than those of race 56 about 18 days after inoculation and at 20°C about 13 days later (Figure 13).

iii) Relationship between pustule size and infection density

Experiments on the relationship between pustule size and infection density on seedlings of Little Club grown at 20°C showed that the pustules were largest when infection density was 1 to 3 pustules per leaf (Table 10). Nine days after inoculation the average size of pustules of race 56 was always larger than that of race 15B-1 (Can.) at all levels of infection density with one exception in experiment 2. Fourteen days after inoculation the pustules of race 15B-1 (Can.) were becoming larger than those of race 56 at all pustule densities except one in experiment 2. It appears that race 56 grows faster than race 15B-1 (Can.) during early stages of rust development but race 15B-1 (Can.) grows faster at later stages and consequently produces larger pustules than race 56.

In experiments on the competitive ability of the normal

Table 10. Relationship between pustule density and size of pustules on the variety Little Club grown at 20°C.

Expt.	Race	Days after inoculation	Pustule density (pustules/leaf)	Total No. of uredia	Total No. of plants	Average size of uredia (mm^2)
I	15B-1	9	1 - 3	17	9	0.39
	"	9	4 - 10	123	18	0.35
	"	9	11 - 30	289	17	0.34
	"	9	31 -	779	16	0.22
	56	9	1 - 3	18	10	0.85
	"	9	4 - 10	119	16	0.72
	"	9	11 - 30	333	21	0.52
	"	9	31 -	778	16	0.29
	15B-1	14	1 - 3	28	13	7.38
	"	14	4 - 10	55	9	3.63
	"	14	11 - 30	389	20	1.10
	"	14	31 -	237	6	0.63
	56	14	1 - 3	26	12	7.13
	"	14	4 - 10	36	6	3.12
	"	14	11 - 30	296	15	1.02
	"	14	31 -	391	10	0.50
II	15B-1	9	1 - 3	11	6	0.51
	"	"	4 - 10	55	7	0.41
	"	"	11 - 30	41	3	0.43
	"	"	31 -	413	7	0.16
	56	9	1 - 3	18	9	0.96
	"	"	4 - 10	86	12	0.58
	"	"	11 - 30	55	3	0.36
	"	"	31 -	370	6	0.22
	15B-1	14	1 - 3	6	3	5.38
	"	"	4 - 10	26	4	1.53
	"	"	11 - 30	152	8	0.75
	"	"	31 -	218	5	0.46
	56	14	1 - 3	5	3	2.79
	"	"	4 - 10	30	7	1.85
	"	"	11 - 30	26	2	0.72
	"	"	31 -	286	5	0.35

colored races and the grayish-brown mutant, the size of pustules on the heavily and lightly infected leaves was measured in the usual way. The results shown in Table 11 indicate that at 15° and 20°C the pustule size of the mutant was not influenced by the density of pustules to the same extent as races 15B-1 (Can.) and 56. Especially, the average size of pustules of the mutant in the mixed infection at 10 days after inoculation at 15°C was not changed by infection density.

Table 11. The average size of uredia in mixtures of the normal races and the grayish-brown mutant.

Race Mixture	Temp. (°C)	Pustule density[1)]	Average size of uredia (mm^2)[2)] normal	mutant
15B-1 + mutant (Can.)	15	Light	0.16	0.15
56 + mutant	15	Light	0.34	0.14
15B-1 + mutant (Can.)	15	Heavy	0.13	0.14
56 + mutant	15	Heavy	0.20	0.14
15B-1 + mutant (Can.)	20	Light	0.72	0.55
56 + mutant	20	Light	0.93	0.46
15B-1 + mutant (Can.)	20	Heavy	0.32	0.28
56 + mutant	20	Heavy	0.33	0.29

1) Light: less than 10 pustules/leaf, Heavy: more than 100/leaf.

2) Size of pustules grown at 15°C was measured 12 days after inoculation.
Size of pustules grown at 20°C was measured 10 days after inoculation.

The results on the relationship between pustule density and pustule size apparently indicate that pustule size of races 15B-1 (Can.) and 56 is influenced by infection density and the size is reduced gradually as infection density increases. The pustule size of race 56 was larger than that of race 15B-1 (Can.) in all infection densities at 9 days after inoculation but 14 days later race 15B-1 (Can.) became larger at all levels of infection density. The results in the experiment on the grayish-brown mutant and the normal colored races indicate that pustule size of the mutant is not influenced much by infection density. This fact suggests that on heavily infected plants the competitive ability of the mutant is not impaired as much as the competitive ability of the normal races.

Incubation Period

To determine the incubation period, that is, the time from inoculation to breaking of host epidermis, the opening of pustules on seedlings of Little Club infected heavily and lightly with each race and grown at 15° and 20°C was observed every day from 6 to 15 days after inoculation.

Pustules of race 56 broke through the epidermis about two days earlier than those of race 15B-1 (Can.) at both temperatures (Table 12). At 15°C the breaking the epidermis was delayed about 5 days in comparison with that at 20°C. Race 56 and the grayish-brown mutant showed a similar tendency in the incubation period,

but the pustules of race 56 opened a little earlier than those of the mutant. Generally, pustules opened earlier on the basal area of leaves than near the tips, and broke the epidermis earlier in heavy infection than in light infection. First opening of pustules of race 56 was on the fifth day after inoculation at 20°C and on the ninth day at 15°C but pustules of race 15B-1 (Can.) first opened on the seventh day at 20°C and the eleventh at 15°C. All pustules of race 56 were open on the fifteenth day at 15°C and the eleventh at 20°C, whereas, those of race 15B-1 (Can.) were open on the sixteenth at 15°C and the twelvth day at 20°C. The results point out clearly that the incubation period of race 56 is shorter than that of race 15B-1 (Can.) at low and moderate temperatures. In other words, race 56 can disseminate urediospores earlier than race 15B-1 (Can.).

Spore Producing Ability

The spore producing ability of races 15B-1 (Can.) and 56 was investigated by inoculating seedlings of Little Club wheat lightly with spore suspension with known amounts of urediospores (7 or 8 mgs) and collecting urediospores by shaking the plants and weighing the spores. At the same time, the number of pustules on the same plants were counted. The experiments were repeated. The results given in Tables 13, 14, and 15 show that in all experiments race 56 produced urediospores more abundantly than race 15B-1 (Can.) at 15° and 20°C. The conclusion may be drawn that race 56 produces urediospores earlier and more abundantly than race 15B-1 (Can.) in uredia grown at low and moderate temperatures.

Table 12. Incubation periods of races 15B-1 (Can.), 56 and 15 (grayish-brown mutant)

Temp. (°C)	1) Days	Percentage of opened pustules: Race 15B-1 (Can.) Light	Heavy 2) (Base)	Heavy 3) (Top)	Race 56 Light	Heavy (Base)	Heavy (Top)	Mutant Light	Heavy (Base)	Heavy (Top)
	9	-	-	-	1.7	2.3	0.0	-	-	-
	10	0.0	0.0	0.0	5.4	3.6	1.0	6.0	3.2	1.7
	11	0.0	2.6	0.4	30.7	38.9	19.6	6.4	16.7	10.8
15	12	12.0	31.9	15.3	54.4	83.5	58.8	26.6	89.4	72.4
	13	41.0	57.5	25.9	88.1	96.6	90.9	85.6	98.9	94.2
	14	73.4	97.2	86.6	95.5	99.2	93.1	97.0	100.0	99.6
	15	95.1	-	-	-	-	-	-	-	-
	6	0.0	1.0	0.0	17.1	38.8	23.5	4.8	7.8	5.6
	7	1.4	20.5	7.0	60.7	77.6	63.2	57.9	72.3	62.1
20	8	40.1	54.1	43.4	81.0	92.6	73.1	87.5	97.1	93.4
	9	61.4	85.7	81.4	93.6	98.2	96.9	95.1	99.3	96.5
	10	88.4	94.5	91.1	97.9	99.2	98.2	98.2	99.8	98.7
	11	93.9	97.2	94.3	-	-	-	-	-	-

1) Days after inoculation.
2) Base of leaves.
3) Top of leaves.

Table 13. The spore-production of races 15B-1 (Can.) and 56 on Little Club seedlings grown at 20°C.

Race	No. of plants used	No. of pustules used	Average No. of pustules/ leaf	Total spore-weight (mgs)	Spore-weight per uredium (mgs)
15B-1 (Can.)	184	1166	6.3	80.3	0.07
56	160	1574	9.8	138.1	0.09

Weighed at 12 days after inoculation.

Table 14. The spore-production of races 15B-1 (Can.) and 56 on different wheat varieties grown at 15°C and 20°C.

(Inoculum density: 8 mgs/24 pots/80cc 1% Tween 20)

Race	1) Host	Temp. (°C)	2) Days	Total No. of plants	Total No. of uredia	Pustules/ leaf	Spore-weight/ uredium (mgs)
15B-1 (Can.)	LC	15	16	100	223	2.2	0.007
56	LC	15	16	84	451	5.4	0.046
15B-1 (Can.)	LC	20	13	69	368	5.3	0.041
56	LC	20	13	82	504	6.1	0.073
15B-1 (Can.)	RB	15	16	87	750	8.6	0.006
56	RB	15	16	104	491	4.7	0.018
15B-1 (Can.)	RB	20	13	78	176	2.3	0.032
56	RB	20	13	67	300	4.5	0.066
15B-1 (Can.)	MA	15	16	89	1192	13.4	0.018
56	MA	15	16	90	1274	14.2	0.035
15B-1 (Can.)	MA	20	13	64	615	9.6	0.027
56	MA	20	13	68	1035	15.2	0.061

1) LC: Little Club, RB: Red Bobs, MA: Marquis.

2) Days after inoculation.

Table 15. The spore-production of races 15B-1 (Can.) and 56 on different varieties grown at 15° and 20°C.

(Inoculum density: 7 mgs/24 pots/80 cc 1% Tween 20)

Race	1) Host	Temp. (°C)	2) Days	Total No. of plants	Total No. of uredia	Pustules/ leaf	Spore-weight/ uredium (mgs)
15B-1 (Can.)	LC	15	16	76	84	1.1	0.022
56	LC	15	16	87	95	1.1	0.026
15B-1 (Can.)	LC	20	13	68	123	1.8	0.028
56	LC	20	13	80	100	1.3	0.051
15B-1 (Can.)	RB	15	16	87	186	2.1	0.005
56	RB	15	16	98	94	1.0	0.011
15B-1 (Can.)	RB	20	13	79	44	0.6	0.013
56	RB	20	13	85	162	1.9	0.024
15B-1 (Can.)	MA	15	16	72	650	9.0	0.016
56	MA	15	16	70	638	9.1	0.040
15B-1 (Can.)	MA	20	13	75	179	2.4	0.024
56	MA	20	13	70	493	7.0	0.027

1) LC: Little Club, RB: Red Bobs, MA: Marquis.

2) Days after inoculation.

Double Inoculation

The effect of double inoculation by races 15B-1 (Can.) and 56 on survival rate was investigated by inoculating seedlings of Little Club and Mindum wheat with race 15B-1 (Can.) or race 56 prior to inoculation with race 56 or race 15B-1 (Can.). Race 56 always produced more infections than race 15B-1 (Can.) on double inoculated leaves (Table 16). In experiments 1 and 2, at 15° and 20°C, race 56 infections were more numerous when plants were inoculated first with race 56 than when they were inoculated first with race 15B-1 (Can.). However in experiments 3 and 4, the number of infections of race 56 on the leaves inoculated with race 15B-1 (Can.) prior to inoculation with race 56 was greater than those of race 56 on the leaves inoculated with race 56 prior to inoculation with race 15B-1 (Can.). The results with Little Club were very similar to those with Mindum. Evidently, there was no antagonistic effect between races 15B-1 (Can.) and 56 of wheat stem rust.

Table 16. Results of a test for antagonism between races 15B-1 (Can.) and 56.

Expt.	Temp. (°C)	Inoculation First	Inoculation Second	Time[1] (hours)	Number of[2] infections 15B-1 : 56	Ratio of survivals 15B-1 : 56
I	15	15B-1	56	24	82 : 107	1 : 1.3
	"	56	15B-1	"	12 : 28	1 : 2.3
	20	15B-1	56	"	52 : 59	1 : 1.1
	"	56	15B-1	"	46 : 107	1 : 2.3
II	15	15B-1	56	24	142 : 170	1 : 1.2
	"	56	15B-1	"	102 : 161	1 : 1.6
	20	15B-1	56	"	111 : 150	1 : 1.3
	"	56	15B-1	"	60 : 102	1 : 1.7
III	15	15B-1	56	24	91 : 413	1 : 4.5
	"	56	15B-1	"	198 : 212	1 : 1.1
	"	15B-1+56		"	57 : 72	1 : 1.3
	"		15B-1+56	"	43 : 89	1 : 1.9
	20	15B-1	56	"	207 : 410	1 : 2.0
	"	56	15B-1	"	249 : 296	1 : 1.2
	"	15B-1+56		"	125 : 191	1 : 1.5
	"		15B-1+56	"	150 : 260	1 : 1.7
IV	15	15B-1	56	48	34 : 125	1 : 3.7
	"	56	15B-1	"	38 : 73	1 : 1.9
	"	15B-1+56		"	4 : 6	1 : 1.5
	"		15B-1+56	"	15 : 20	1 : 1.4
	20	15B-1	56	"	44 : 223	1 : 5.1
	"	56	15B-1	"	238 : 232	1 : 1
	"	15B-1+56		"	39 : 46	1 : 1.2
	"		15B-1+56	"	19 : 45	1 : 2.4

1) Time between the first and the second inoculation.
2) Number of infections on mindum leaves.

DISCUSSION AND CONCLUSIONS

Previously investigators have reported on the basis of field survey that in North America the predominance and distribution of physiologic races of wheat stem rust, P. graminis f. sp. tritici, have varied year after year (9, 13, 14, 16, 17, 18, 22, 24, 25, 27, 28, 29, 30, 31, 32, 33, 42, 44, 45, 50, 51, 52, 53, 54, 55). They suggested that causes for predominance of physiologic races of wheat stem rust in nature may be seasonal temperature (52), distribution of wheat varieties (24, 54), conditions affecting the winter survival and subsequent development and dissemination of inoculum of different races from the far South (55), and the relative amounts of different races produced on barberries and disseminated from them (42). Watson (59) concluded from greenhouse experiments that predominance of a race depends on the amount and character of each rust race present in the mixture, the variety and temperature. Loegering (38) suggested that the concurrence of a number of relatively minor factors may bring about cumulative results when operating together for several successive generations, even though their effects might not be apparent in a single generation and that a combination of relatively minor ecological factors, when operating together, affect the success or failure of physiologic races in nature.

Competitive ability:

In the experiments on competitive ability of races 15B-1 (Can.) and 56, predominance of a race in mixed infections was greatly influenced by temperature and pustule density. Race 56 generally predo-

minated over race 15B-1 (Can.) in the mixtures at higher temperatures but not at low temperature (Figures 3, 4, and 5). In other words, race 15B-1 (Can.) is superior in competitive ability at low temperature. Stakman et al. (52) reported that race 56 could compete very effectively with other races when they were associated in culture at high temperatures. This fact agrees with the present experimental results. Watson (59) observed that temperature was found to influence the variety on which a mixture was grown and in this way to affect the final composition of the mixture of wheat stem rust races. However, Thurston (56) reported that tests at two different temperatures revealed very little difference in the final proportions of races of Phytophthora infestans in mixture. The difference between the results mentioned above may be due to different fungi and the combination of races tested. It can be concluded from these studies that the competitive ability of races is influenced by temperature but temperature effect may differ in different combinations of mixed races.

In Figure 17 an attempt has been made to relate the mean temperatures in Manitoba for June, July and August (4, 5) with the relative distribution of races 15B (including sub-races), 15B-1 (Can.), and 56 in Manitoba from 1949 to 1964 on the assumption that the data obtained from the isolates of races 15B-1 and 56 studied (13, 14, 16, 17, 18, 24, 25, 27, 28, 29, 30, 31, 32, 33, 44, 45, 50) are generally applicable to these races as they appeared in the field during the period mentioned above.

It appears to be significant that the two years of excessively

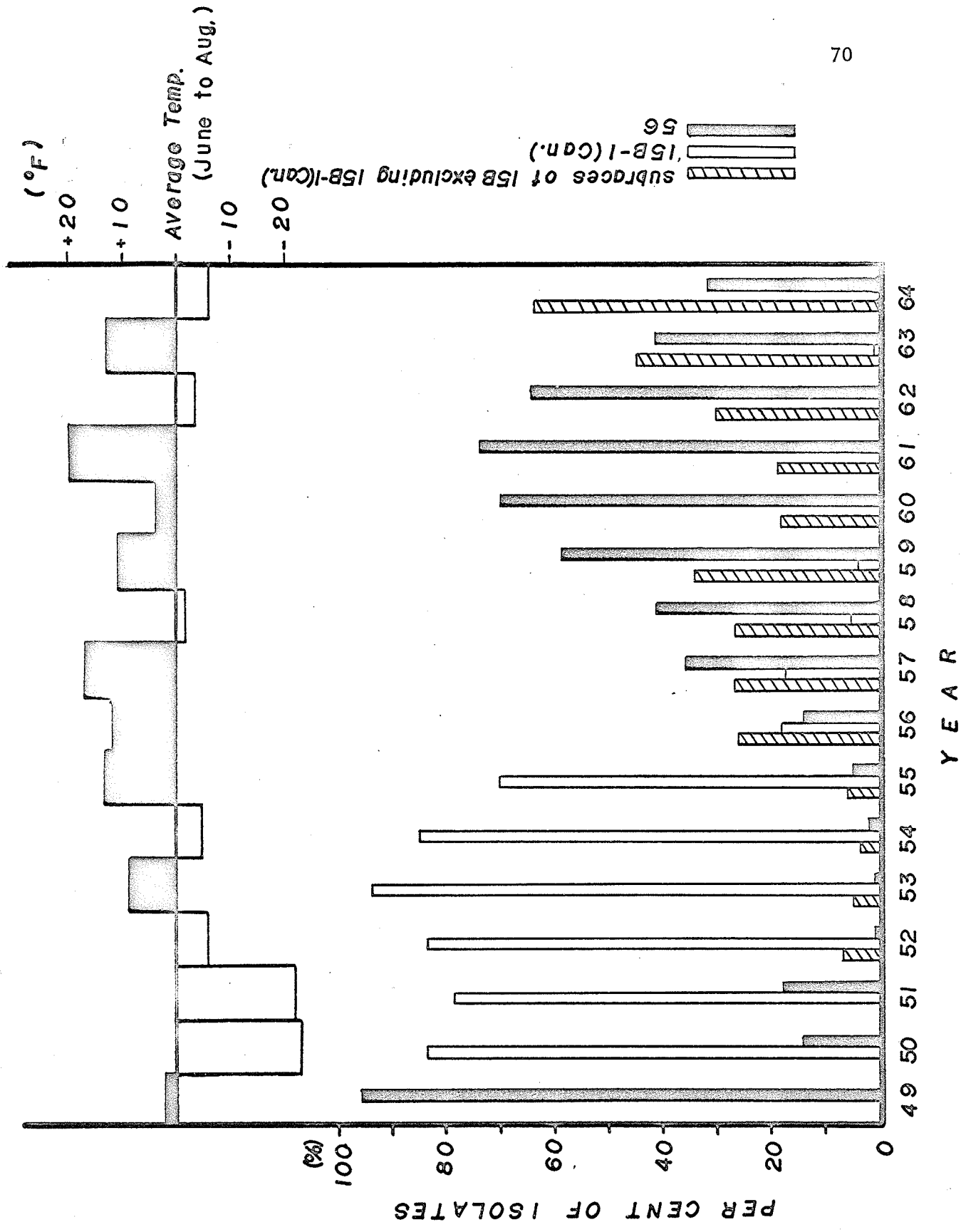


Figure 17. Relative prevalence of races 56, 15B-1 (Can.) and other subraces of 15B in Manitoba in relation to fluctuation of average annual temperature for June, July, and August about the long time mean.

low summer temperature, 1950 and 1951, are the years in which race 15B became the predominant stem rust race. It may also be significant that the three years of excessively high temperature, 1955-1957, are years in which race 56 made a gradual recovery from its extreme low incidence during the years 1952-1954. Again, it may be significant that race 56 rose once more to high predominance during the warm summers of 1959-1961 when the incidence of race 15B was low.

In the present investigation, pustule density on the host variety had a remarkable effect on the competitive ability of races. The results show that at 15° and 20°C race 15B-1 (Can.) in mixed infections on heavily infected plants predominated generally over race 56 (Figures 8a and 9a), whereas race 56 was more prevalent in mixtures on lightly infected leaves of Little Club and Red Bobs wheat (Figures 8b and 9b). In the experiments on the competitive ability of a grayish-brown mutant and normal colored races, the infection density also affected the competitive ability of the races (Figures 10a, 10b, 11a, and 11b). Previous reports regarding the competition between races have not dealt much with pustule density on plants. Loegering (38) only mentioned that the average number of infections per leaf of differential host was approximately 40. The infection densities used in the present study were less than 10 pustules per leaf as light infections and more than 100 pustules per leaf as heavy infections. A possible explanation of the superiority of race 15B-1 (Can.) is that its ability to take nutrients from the host infected heavily with the mixture may be greater than that of race 56, while on lightly infected plants the

ability of race 56 may be greater.

The competitive advantage shown by race 15B-1 (Can.) over race 56 in the above-mentioned experiments under conditions of heavy infection raises the question of what advantage this would confer on race 15B under natural conditions if the behavior of this race in the experiments is applicable to race 15B in the field.

It would be expected that in the initial stages of an epidemic race 56 would develop more rapidly on varieties susceptible to both races. However, when pustule density reaches a fairly high level it is likely that race 15B would increase at a greater rate and assume predominance by the time rust infection had reached an epidemic level.

Such a competitive advantage could not be the reason for the high prevalence of race 15B in Manitoba and Saskatchewan because most of the wheat varieties grown in that area are fairly resistant to race 56 and most races other than race 15B. But it could be the reason for prominence of race 15B in epidemic years in areas farther south where varieties susceptible to both races 15B and 56 have been grown. As the racial composition of an epidemic is largely determined during its northward progress through the Mississippi valley any competitive advantage that race 15B might have in the Great Plains region farther south would be reflected in the race distribution in Western Canada.

The host varieties used in the investigation influenced only slightly the competitive ability of the races (Figures 3 and 5) the chief effect being on relationship between pustule density and the competitive ability (Figures 8a and 9a).

In early works on competition among races of the rusts, effect of host variety on competitive ability was shown (38, 59). In nature, the host varieties may contribute largely to shifts in the relative prevalence of rust races (24, 38). Obviously, a race cannot become prevalent unless it can attack host plants. An interesting point in the present experiments was that the races showed the same competitive ability on Marquis wheat which shows 4- type of rust reaction to race 15B-1 (Can.) and 3+ type to race 56 as on Little Club wheat, which shows 4 type reaction to both races (Figures 3 and 4). Therefore, it may be supposed that a slight difference in susceptibility of wheat varieties to races may not much influence the competitive ability of the races.

In order to explain the causes of predominance of a race, the behavior of races 15B-1 (Can.) and 56 was studied in relation to spore-germinability, spore-longevity, host infection, growth of pustules, incubation period, spore-production, nutrient effect on rust development and double inoculation. These aspects of the problem will be discussed in this sequence.

Germinability:

It seems that urediospore germination and germ tube growth may be factors in competition between races in the uredial stage. A race, whose urediospores germinate faster on the host plants and have a higher rate of germination, may have an advantage in establishment of infection in the host plants over other races which germinate slowly and have inferior spore-germination.

In germination tests on 1% water agar, urediospores of race 15B-1 (Can.) germinated slightly better and faster than those of race 56 at several different temperatures (Table 5). A temperature of 20°C was most favorable for germination on the water agar for both races. Urediospores of both races, however, germinated equally well when the spores were seeded on the wet under-surface of wheat leaves. Cassell (7) observed that spore germ tubes of race 56 developed faster than those of all other races tested at 20°C and race 56 was next to race 36 in ability to develop at high temperature and was the least adapted to cold. These results are in agreement with the present studies in which race 56 became predominant over race 15B-1 (Can.) in mixed infections at higher temperatures (Figures 3, 4, and 5). However, Line and Bugbee (37) concluded that the aggressiveness of race 56 must be due to factors other than the ability of urediospores to germinate at low temperatures. In the present study, germinability of races 15B-1 (Can.) and 56 was not much different on wet leaf surfaces over a range of temperature. Therefore it may be concluded that germinability did not greatly influence competitive ability in this investigation.

Spore-longevity:

Spore-longevity may be one of factors affecting predominance of a race in nature. A race with greater spore-longevity may have an advantage in infecting host plants in nature. Spore-longevity, however, was not a factor in this investigation on the competition between races because fresh urediospores were always used as experi-

mental material.

Infectivity:

The infective ability of races 15B-1 (Can.) and 56 to Little Club wheat appeared to be the same in the experiment on single spore infection but the infection rate was very low (2.3%). The percentage of rust urediospores infecting the host have been reported variously as 0.7 by Petersen (43), 1 by Levine (36), 4.5-7.3 by Miller (41), 5-10 by Rowell et al. (49) and 88 by Durrell and Parker (11). Some of these results are in agreement with the low infection rate shown in the experiment on single spore infection in this study.

Inoculum density must be considered in this kind of experiment because generally as inoculum density is increased the number of uredia on leaves increase linearly until a point is reached beyond which increases in inoculum density have no effect on the number of uredia (10, 48). In the present experiment, inoculum density was moderate (number of infections were 2 to 30 per leaf).

The present studies showed that infective ability of race 56 was greater than that of race 15B-1 (Can.) on the wheat varieties tested (Tables 8a and 8b). Previous reports have indicated that races 17 and 147 caused fewer infection centers on Marquis, Arnautka, Einkorn, and Vernal wheat varieties than did races 19 and 56 (59), and that infective ability of varieties to a race may differ (8, 20). In the present experiment, the seedlings of Marquis wheat were generally the most highly infected by both races and the Mindum variety was the least.

In this experiment, correlation between the number of urediospores and spore-weight of each race was not investigated. Therefore, the infective ability of both races mentioned above might be over- or under-estimated if the number of urediospores in a definite spore-weight differ in the two races. However, in the absence of evidence that races differ in the mass of their urediospores this possibility is ignored in the interpretation of the results obtained here.

The infectivity of races was slightly influenced by temperature in some experiments (Tables 2, 8a, and 8b). In general, the higher the temperature at which seedlings infected with each race were kept, the fewer pustules developed on the plants. Other studies (28, 35, 40) have shown that races of wheat stem rust differed in ability to produce infections on host plants at low temperature (40) and at high temperature (26). Cassell (6) reported that race 36 caused the heaviest infection at moderate to low temperature while race 56 caused the heaviest infection at moderate to high temperature. This evidence supports the present investigation on the competitive ability of races 15B-1 (Can.) and 56, in which race 56 was predominant over race 15B-1 (Can.) at high temperature. The importance of the host variety-rust race combination in assessing the effect of temperature has been pointed out (15) but in this investigation race 56 was usually superior in infective ability on all the host varieties at low, moderate, and high temperatures.

The fact that isolates of wheat stem rust can be selected

for abilities to germinate, to infect, and to develop at low temperature (47) suggests that the abilities are genetically controlled and therefore would be factors in the natural selection of temperature-adapted strains.

Growth of pustules:

The initial growth of pustules of race 56 was faster than that of race 15B-1 (Can.) at three different temperatures (Figures 13 to 16). At later stages of development the pustules of race 15B-1 (Can.) were larger than those of race 56. The pustule size of race 15B-1 (Can.) exceeded that of race 56 sooner at high temperature than at low temperature. The rate of pustule development at early stages would influence competition between races. The race which grew faster at early stages of pustule development may be a better competitor than another race which grew slowly because of its more rapid production of spores.

Rapid spore production may be one of the causes for aggressiveness of race 56 in mixed infections. In the experiments at higher temperatures the mixed spores were collected 14 days after inoculation in each uredial generation. At that time, each pustule of race 56 was larger than that of race 15B-1 (Can.).

Infection density evidently influenced the pustule size in both races (Table 10). Yarwood's finding (62), that the diameter of mycelium and sporulating area of pustules of Uromyces phaseoli decreased as the number of pustules per unit area increased, completely agrees with the result in the present study. The

experiment on relationship between pustule density and pustule size also showed that at the first stages of rust development race 56 grew faster than race 15B-1 (Can.) but race 15B-1 (Can.) grew faster than race 56 at later stages of growth. The experiment on effect of infection density on the competitive abilities of races 15B-1 (Can.) and 56 indicated that at high pustule density race 15B-1 (Can.) generally predominated over race 56 (Figures 8a, 8b, 9a, and 9b). This result cannot be explained clearly by the observations on the relationship between pustule density and pustule size. However, the results (Table 11) on the relationship between infection density and pustule size in mixtures of normal colored races and the grayish-brown mutant indicate that when infection density is great the average size of pustules of race 15B-1 (Can.) grown at 20°C was almost the same as that of race 56 but race 56 produced larger pustules than race 15B-1 (Can.) when infection density was light. This finding may explain the high prevalence of race 56 under conditions of light infection.

Incubation period:

The incubation period (the time between inoculation and breaking of the host epidermis by the rust) of race 56 was shorter than that of race 15B-1 (Can.) at 15° and 20°C (Table 12). In general, the incubation period of race 15B-1 (Can.) was about two days longer than that of race 56. The opening of pustules at 15°C was a few days later than at 20°C. The results indicate that different races differ in incubation period. This may be an

important factor for predominance of a race because the race with the shorter incubation period can disseminate urediospores more rapidly after infection. When pustules first break the epidermis and when all pustules finally break out depend on the temperature at which plants are grown and the infection density and infection position on the plants. The results of the present studies and those of Yarwood (62) showed that pustules opened sooner in heavy infection than in light infection. This finding indicates that a race disseminates urediospores rapidly when heavy infection occurs on host plants. The rapid dissemination of urediospores, which is closely related to length of incubation period and to growth rate is, therefore, one of the important factors for predominance of a race.

Spore-production:

The ability to produce many urediospores is one of most important factors for competition with other races. The finding (Tables 13, 14, and 15) that race 56 usually produces more urediospores than race 15B-1 (Can.) agrees with the observations demonstrating that race 56 grows faster than race 15B-1 (Can.) and has a shorter incubation period. Investigations regarding relationships between urediospore production and humidity, pustule density, and age of infection (62), the number of urediospores per uredium (2, 22, 51), and rate of spore production (9, 12) were reported. However, there was no information concerning the relative spore producing abilities of different races of wheat stem rust.

Double inoculation:

There was no antagonistic effect between races 15B-1 (Can.) and 56 (Table 16) in the experiment reported here. Previously, acquired immunity to a race of Uromyces phaseoli (60) and antagonistic effect of filtrates of sporangial suspensions of Phytophthora infestans (56) have been reported but no antagonistic effect was observed between races of wheat stem rust (3). The most interesting report regarding this investigation is Yarwood's (60). He observed that the tissue adjacent to the old infection did not become diseased. The zone of inhibition was wider distally than proximally from the infection area, and its width varied directly with age of the first infection. The average distances in millimeters for total and partial inhibition in one test were 0 and 0 when the second inoculation followed the first by 2 days, 1 and 10 at 5 days and so on. The present experiment did not show any effect of one race on the other. Possibly there is no antagonistic effect, or the time elapsing between the first and second inoculations was not suitable for demonstrating it.

Finally the results from all the experiments in this study are summarized in Table 17. The Table shows that race 56 of wheat stem rust is superior to race 15B-1 (Can.) in various abilities, but inferior in a few characters. Infectivity, growth of pustules, spore-production, and competitive ability may be the most important factors influencing the predominance of races 15B-1 (Can.) or 56. Race 56 appears to have superior capability in each of these factors.

The predominance of a race in a population under artificial

and natural conditions correlates closely with the ability of urediospores to germinate on the host; to maintain spore viability; to infect a host; to attack resistant varieties; to compete for host nutrients (related with infection density); to grow rapidly on the host; to produce many urediospores; and to disseminate spores widely. These abilities may be affected by temperature, other meteorological factors, host variety and the rust itself.

Table 17. Summary of the experiments

Experiments	Race 15B-1 (Can.)	56
Spore germination on water agar	+	-
Spore germination on wheat leaves	=	=
Spore longevity	=	=
Single spore infection	=	=
Infectivity	-	+
Pustule growth at early stages	-	+
Pustule growth at later stages	+	-
Spore-production	-	+
Competitive ability at low temperature	+	-
Competitive ability at high temperature	-	+
Competitive ability at light pustule density	-	+
Competitive ability at heavy pustule density	+	-

+ : Superior
= : Equal
- : Inferior

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