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THEORETICAL AND APPLIED GENETICS

Ploidy and Strain Differences in Seed Germination of *Glycine wightii* at Different pH Levels

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Summary. Seeds from 27 wild strains (18 tetraploids and 9 diploids) of *Glycine weightii* were germinated at a pH range of 5 to 8. The differences in germination (%) between all the strains were highly significant but between pH levels they were only nearly significant (P = 0.067) with no interaction between pH levels and strains. Mean germination (%) for all tetraploids seems to be slightly higher (≃ 2%) than that for all diploids, especially at pH's 5, 7 and 8 but this may be due to the significantly longer time (≃ one day) it took tetraploids to complete germination. The apparent inverse relationship between seed weight and germination (%) was not significant.

Mean germination time was highly significant for strains, pH's and their interaction. Increasing mean germination (%) resulted in decreasing mean germination time among strains. Large seeds took less time to germinate especially those from some of the tetraploid strains. This indicates that it is possible to produce a variety with high germination (%), fast germination rate and possibly large seeds. If the marked difference in pH tolerance among strains will prove to be mainly hereditary, then it will be also possible to select for either specific pH tolerance or tolerance at a wide range of pH.

Key words: *Glycine wightii* – Seed germination – Strain differences – Ploidy – pH – Gene × environment interaction

Introduction

Although pH constitutes a very important component of the plant edaphic environment, studies on its genetic basis are lacking, except for those of Soliman (1976) in the monkey flower and Stølen and Andersen (1978) in barley. Such studies are essential especially when new strains of plants from different geographic origins and possibly different pH requirements are introduced into a breeding program. One such plant is the perennial *Glycine wightii*, native to tropical Asia and South Africa. This legume is now receiving increasing attention in Australia, Africa and South America as a possible valuable supplement to semi-arid and moderately humid tropical and subtropical pastures.

The agronomical advantages of *G. wightii* in relation to other tropical legumes appear to be: 1) high protein content, 2) lower optimum temperature for growth, 3) vigorous growth, 4) high capability for nitrogen fixation, and 5) frost resistance. An added benefit is that milk production in the tropics can approach that of temperate areas if *G. wightii* is used in combination with other pasture forage (Anon. 1967). It is a polymorphic species (Herman 1962) with diploid and tetraploid strains (Pritchard and Wutoh 1964). It has wide strain differences in agronomic [yield (Edye 1967; Funes and Perez 1976), maturity, stolon development and frost resistance (Edye and Kiers 1966)], genetic [flowering time, maturity date, yield, stolon characteristics, seed weight (Wutoh et al. 1968a, b), and nodulation (Diatloff and Ferguson 1970; Nicholas 1971; Nicholas and Haydock 1971)] and physiological [effect of photoperiod and temperature on flowering (Wutoh et al. 1968c)] traits. Some lines of *G. wightii* are also immune to pod mottle virus (Scott et al. 1974).

Nevertheless, there are some limitations, such as slow nodulation and establishment and the need for well-drained soil with a high level of fertility. Soil pH is a crucial factor in relation to soil fertility and nodulation. The effect of pH on Mn toxicity, lime responses, calcium levels and nodulation has been studied by various investigators (Andrew 1976; Andrew and Hutton 1974; Lee and Wilson 1972; Munns et al. 1977a b; Thomas and Whiteman 1971; Truong et al. 1967). Recent studies indicate that the problem of nodulation seems to be solvable by selective breeding since considerable variation among strains of *G. wightii* in nodulation and symbiotic effective-

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Table 1. Origin and available information on the 27 accessions of *Glycine wightii*

Designated number	Introduction number CPI	Origin and available information
Diploid		
1	32939	East Africa. 12 miles from Meri off Meru-Isiolo road
5	30599	Central Regional Research Centre, Ilonga, Tanganyika
11	32940	East Africa. Namanga
16	30396	Centre de Recherches Agronomiques, Bambey, Senegal
17	30365	Division of Crops & Pastures, Department of Agriculture, Pretoria, South Africa, ex Tanganyika
18	30497	Grassland Research Station, Marandellas, Southern Rhodesia. Melsetter, S. Rhodesia. Small seeded variety
19	30498	Grassland Research Station, Marandellas, Southern Rhodesia. Norvals Special
20	32942	East Africa. 12 miles from Namanga inside the Tanganyika border
21	30640	Station Agronomique de Lac Aloatra, Madagascar, ex Mywapwa
Tetraploid		
2	34589	Sao Paulo State, Brazil
3	30360	Division of Crops & Pasture, Department of Agriculture, Pretoria, South Africa. Grassland Selection
4	33159	East Africa. Swamp edge, Mamalu, Uganda
6	30600	Agricultural College & Research Institute, Coimbatore, India
7	30532	Matopos Research Station, Federal Ministry of Agriculture, Southern Rhodesia ex Ford & Co. Johannesburg
8	30471	Tanganyika. ex Masama Kibo Estate, Moshi
9	37922	Grasslands Research Station, Kitale, Kenya. Not entirely cleistogamous
10	26433	Northern Regional Research Centre, Tengern, Arusha, Tanganyika (Group IV)[a]
12	30079	Agricultural Research Station, Lilongwe, Nyasaland, ex N. Rhodesia
13	30359	Division of Crops and Pastures, Department of Agriculture Pretoria, South Africa. ex Nyasaland
14	31639	Gatooma Research Station, Gatooma, Southern Rhodesia
15	17673	Cotton Research Station, Gatooma, Southern Rhodesia (Group II)[a]
22	30077	Agricultural Research Station, Lilongwe, Nysaland. ex Domasi, Nyasaland
23	23411	Estacion Experimental Agronomica, Santiago de las Vegas, Cuba (Group I)[a]
24	30531	Matopos Research Station, Southern Rhodesia, ex Ford & Co. Johannesburg
25	30530	Mt. Makulu Research Station, Northern Rhodesia. Local strain
26	30529	Mt. Makulu Research Station, Northern Rhodesia. Gunsons strain, commercial
27	30638	Station Agronomique de Lac Alaotra, Madagascar

[a] Group classification is obtained from Edye *et al.* (1970)

ness has been demonstrated (Diatloff and Ferguson 1970; Nicholas and Haydock 1971). Increased variation and hybrid vigor for growth and nodulation were also observed in the F_2 generation of a cross between two different strains (Nicholas 1971).

The effect of soil pH on *Glycine* is still not clear. Some investigators found optimum growth at about pH 5 while others reported more neutral or alkaline levels were more favorable (Andrew and Hutton 1974; Anon. 1967). Such discrepancies may be attributed to strain differences, and if so this could be an important trait for selection and inclusion in breeding programs. An added advantage in this respect is Soliman's suggestion that pH tolerance is probably independent of heavy metal tolerance (Soliman 1976).

The aim of this investigation was to study the existence of strain differences in tolerance of *G. wightii* to various pH levels. Another purpose of the study was to correlate the observed differences in pH tolerance (measured by percent germination and mean gemmination time) with that of seed weight. Differences in tolerance to pH were observed in tetraploid and diploid strains with wide geographic background.

Materials and Methods

Eighteen tetraploid and nine diploid strains (introductions) of *G. wightii* from a Townsville 1967 crop (stored at 10°C and 25% RH since harvest) were used. Table 1 shows the number designated to each strain in this experiment, their introduction number, their origins and available information. One hundred unscarified seeds (divided into four replications) of each strain were germinated at pH 5-8. The total number of experimental units used for the analyses were therefore 4 pH's × 27 strains = 108. The 100 seeds were placed on moist blotting paper in squared petri dishes made

of plastic. These dishes were continuously covered to ensure that high degrees of moisture were maintained. They were placed in a growth incubator set at 26°C with high relative humidity which was maintained throughout the experimental period. Shelves within the incubator were rotated daily after counting to ensure uniform experimental conditions. The experiment was run in the dark except when germination was recorded.

pH solutions were initially prepared using NaOH and H_2SO_4 plus 0.001 molar phosphate buffer (KH_2PO_4 and $KHPO_4$) set at pH 7, which acted to stabilize pH values. The effect of variable concentrations of Na and SO_4 imposed by the pH treatment could be ignored since very small amounts of NaOH and H_2SO_4 were used. No fungicide or other ions were added to the pH solutions as an attempt was made to minimize the effects of any such elements on germination. Counts of the number of seeds germinated, hard seeds, and dead seeds for each replication were collected at the same hour daily. From such data, percentage germination and mean germination time up to day 25 were calculated. In statistical analyses, i.e. analysis of variance and regression, the angular values of percent germination were used.

Weight g/100 seeds from each strain, en masse, ignoring intra-strain variation, was also obtained.

During the course of the experiment it was noted that the pH of the prepared solutions did not remain constant. Therefore, a separate trial was conducted to determine accurately the change that occurred in pH. Petri dishes and wadding were treated with buffers of pH 5-8, under conditions similar to those of the main experiment (but without seeds) and were checked daily for deviations from the desired pH. Results of this trial are shown in Figure 1. Perhaps the best explanation of this phenomenon is that the buffer used was most effective at pH values around 6.5 and least effective with increasing deviation from this value. However, by the tenth day when most of the seeds were germinated, there was still an obvious difference between the four pH levels.

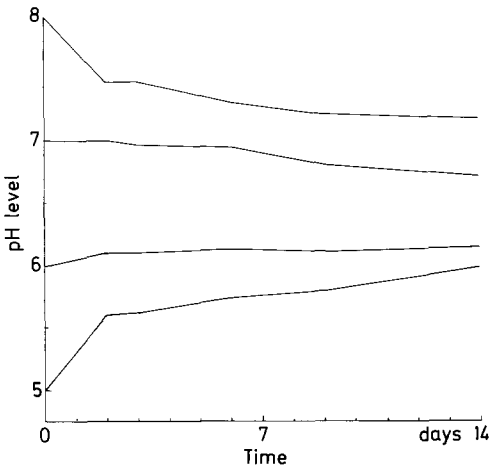


Fig. 1. Variation in pH of the germinating solution due to time

Results

Percent Germination

The results of the analysis of variance of the angular transformed values of percent germination indicated that strains were the only significant factor ($P < 0.01$). The wide range of difference (10%-83%) among strains is shown in Figure 2a and b. Differences among the four pH levels were nearly significant ($P = 0.067$). If the pH range had not been narrowed, as shown in Figure 1, the difference might have been greater. The apparent interaction between pH level and percent germination (Fig. 2a and b) was not significant, however, different strains showed different pH tendencies. Also, different strains had their maximum percent germination at different levels of pH while in other strains germination declined steadily from pH 5 to pH 8.

Mean Germination Time

The analyses of variance of mean germination time, its log and square root gave similar results. Highly significant differences were found among pH's, among strains and for pH/strain interaction ($P < 0.01$). Duncan's multiple range test at the 0.05 level indicated that pH 7 is significantly different from all other pH's. From Figure 3a and b the magnitude of the differences and interaction can be easily recognized.

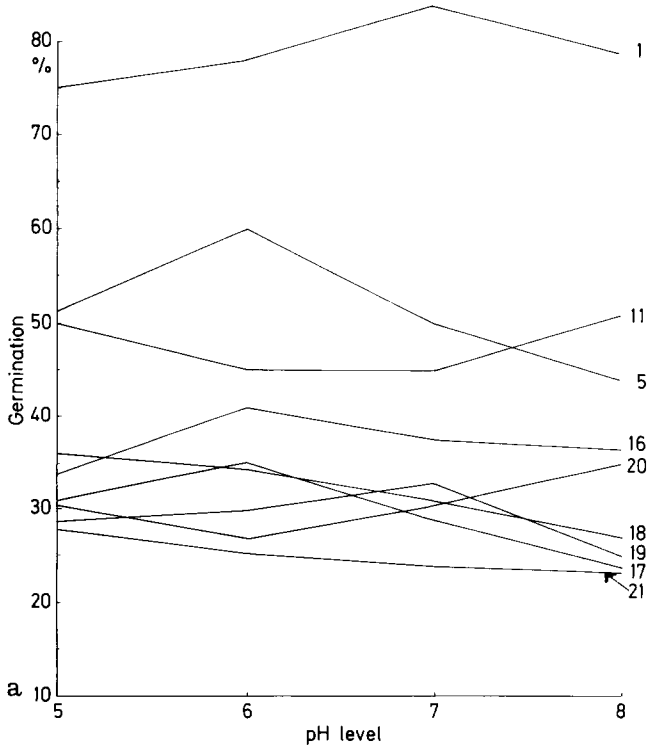
In general, germination was faster at neutral pH and slower at extremes. However, in some strains this trend was reversed (strains 14 and 12). For the strains that showed fast germination (1 and 5) the differences between pH levels were small but the differences between pH's within strains increased with increasing germination time between strains (Fig. 3b).

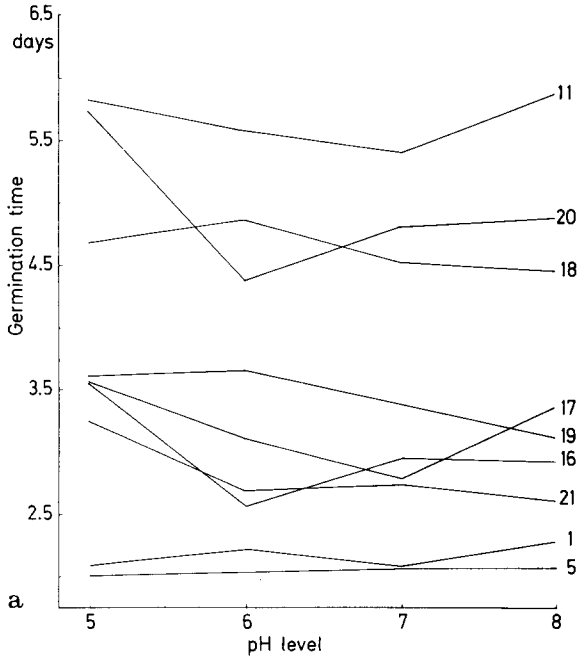
Relationship Between Seed Weight and Germination

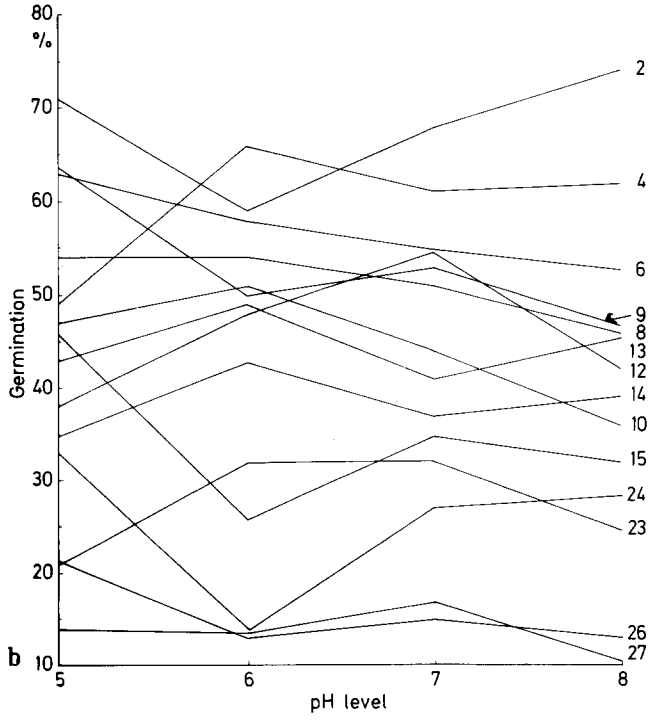
The results showed consistent negative correlation between seed weight and either mean germination time or percent germination for each pH. This relationship was significant for mean germination time at pH 5 and 7 ($P < 0.05$) and nearly significant at pH 6 and 8. This significant relationship became more pronounced ($P < 0.001$) when all pH's were included (degrees of freedom were increased from 25 to 106). These results indicate the presence of an inverse relationship between seed weight and germination time. The degree of determination r^2 is low (= 0.11) i.e., only 11% of the variation in germination time can be attributed to variation in seed size. This relationship may be partly genetic and partly physiological.

Percent germination was not significantly correlated with seed weight.

The distribution of germination time of strains at pH 5 against seed weight is depicted in Figure 4. There is a noticeable gap in seed weight between 6 and 7 grams per 100 seeds, as none were present in the sample of seeds used. The log of seed weight and the inversed squared or







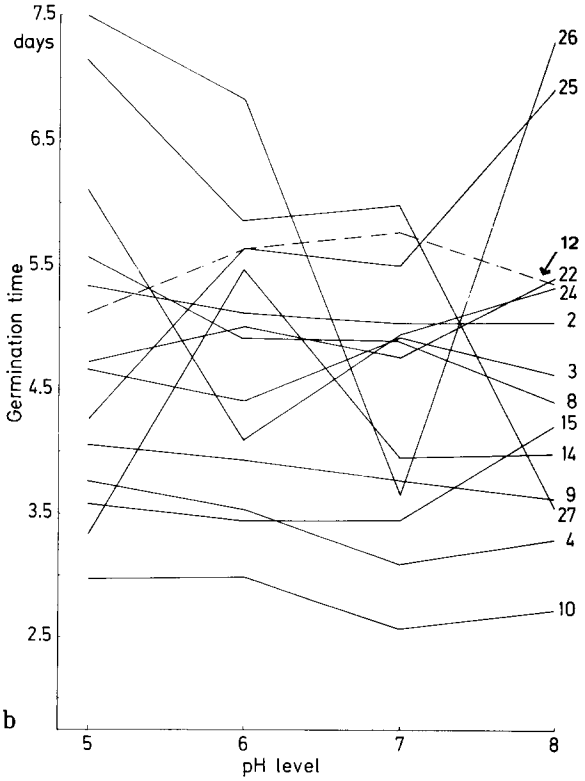


Fig. 2a and b. Percent germination of *Glycine wightii* at various pH levels. a for 9 diploid strains, b for 14 tetraploid strains of (Strain 2 is similar to 3, strain 8 is similar to 7, and strain 24 is similar to 22 and 25)

Fig. 3a and b. Mean germination time of *Glycine wightii* at various pH levels. a for 9 diploid strains, b for 14 tetraploid strains of (Strains 23, 22, 13 and 6 are similar to 15, 7, 3 and 4 respectively). The use of the broken line is for clarity

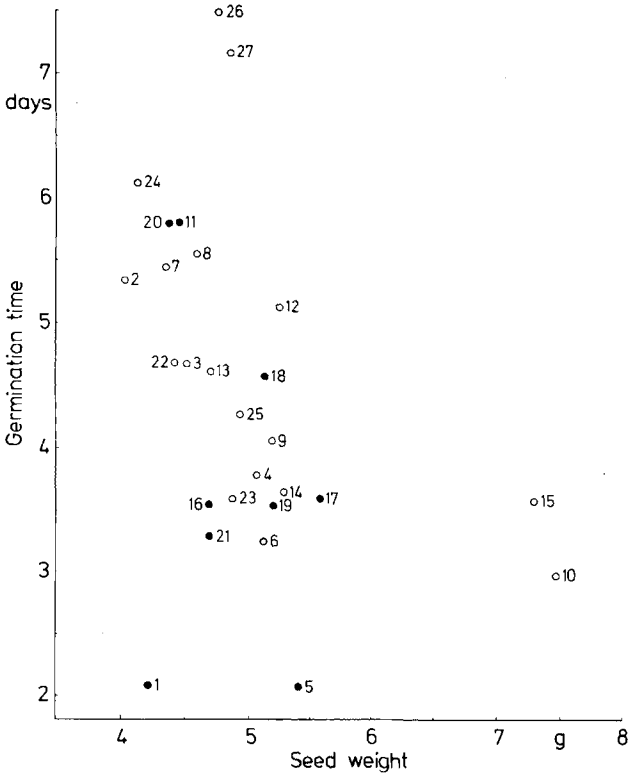


Fig. 4. Relationship between mean germination time and weight of 100 seeds of 27 strains of *Glycine wightii* at pH 5. Solid symbols represent diploid and open symbols, tetraploid strains

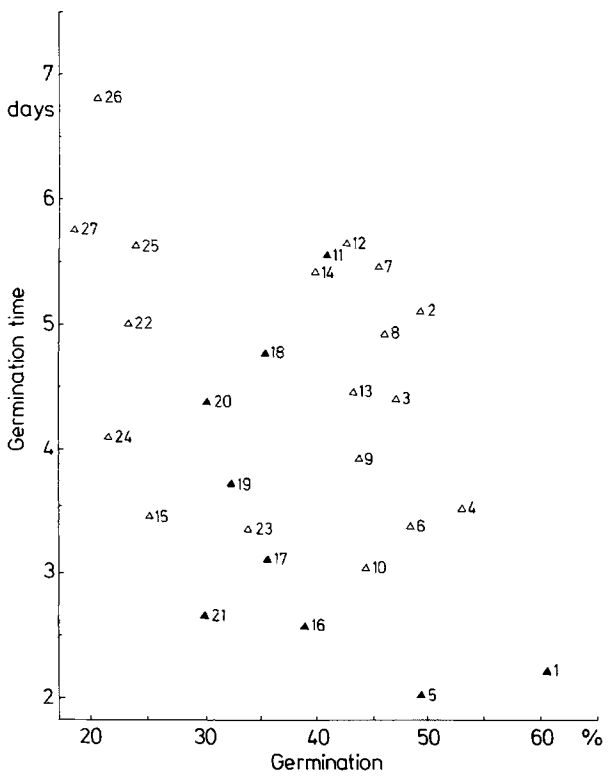


Fig. 5. Relationship between mean germination time and percent germination of 27 strains of *Glycine wightii* at pH 6. Solid symbols represent diploid and open symbols, tetraploid strains

cubed values of seed weight were tried for a closer fit, but they produced less significant results.

A regression of percent germination on mean germination time also showed a consistent negative relationship. This was significant between means of each strain at pH 6 ($P < 0.05$) and for the total across all pH's ($P < 0.005$), indicating that strains with lowest percent germination tend to have longer mean germination time (Fig. 5).

Discussion

The results obtained in this experiment indicate strain differences and differences between tetraploids and diploids in pH-tolerance measured by seed germination in *G. wightii*. As expected for physiological and fitness characters there is a large strain by environment (pH) interaction for mean germination time. These results are in agreement with those of Soliman (1976) working with root growth of heavy-metal tolerant and non-tolerant strains of the monkey flower *Mimulus guttatus* and their hybrids grown at different pH levels. It might be argued, however, that the observed strain differences may be due to factors other than genetical, even though all the original seeds were obtained from plants grown under presumably the same field conditions. To establish that the observed differences are genetically controlled, it would be necessary to cross extreme strains to obtain their F_1 and F_2 and compare the behaviour of the parental types, their hybrids and segregations in F_2, at various levels of pH. Recently, Stølen and Andersen (1978) demonstrated that tolerance to high soil acidity in barley is controlled by a single dominant gene.

Thomas and Whiteman (1971) studied seedling emergence and found it inversely related to the content of clay plus silt. If their results are compared to the pH of the soils a trend similar to that of strains 2, 11, 20 and 24 (Fig. 2a, b) is found with higher germination at extreme pH's.

The direct effect of pH, due to toxicity of the hydrogen ion, is on the sensitive root cells (Russell 1961). However, under natural conditions and in the field, pH may also affect the solubility of toxic minerals as well as essential nutrients, therefore influencing their availability to the plant roots (Buckman and Brady 1969). Accordingly, the strain differences and their interaction with pH may reflect the evolutionary history of each strain in its original and specific environment.

When ten tropical legumes were evaluated for adaptability, *G. wightii* was the most stable legume with wide

edaphic adaptability (Garter et al. 1974). Within this species the 'Clarence' cultivar was generally adaptable while 'Tineroo' was specifically adapted to high-yielding environment. In the present experiment some strains (Fig. 3a and b) showed no differences in mean germination time at different pH levels, in other words, they are stable (adapted to fluctuating pH) regardless of their percent germination. Other strains showed faster germination rate at specific pH's, e.g. strains 12, 14, 25, 26 and 27 (Fig. 3a and b) showed no differences in mean germination ables are never constant for any period of time it is then important in any breeding program to select for fast germination over a wide range of pH, e.g. strains 1 and 5. Fortunately, as indicated in this experiment (Fig. 5) fast germination seems to be associated with high percentage of germination ($r = -0.27$, $P < 0.005$). Also, short germination time will result in the plant establishing itself quickly.

Seeds could also change the pH of their germination media (Crocker and Barton 1957). Soybeans decreased the pH of aluminium solution from 4.5 to 3.6 after three minutes, then returned it to its original level within 12 minutes and subsequently increased the pH to 5.8 in 60 minutes, where it stayed for the next 18 hours when the experiment was terminated. This believed to be an influence of the nature of the protein (proteases) in the seed. Differences in such proteins, which are under genetic control, undoubtedly result in strain differences in sensitivity to pH.

Since the number of strains is relatively large, the phenotypic correlation among strains at a given pH could be considered as a genetic correlation in the broadest sense. Although there is an inverse correlation between mean germination time and seed weight, where small seed size is associated with long germination time, it is not large, indicating that it is probably due to linkage rather than pleiotropy. This is an advantage. Hutton (1965) and Diatloff (1974) suggested that by selecting for variaties of *Glycine* with larger seeds the problem of slow seedling establishment and nodulation might be overcome. Examination of Figure 4 indicates that strain 1 (diploid) germinates quickly with light seeds and strain 10 (tetraploid) germinates quickly with large seeds. To investigate this relationship in detail the behaviour of individual segregants from a cross between extreme genotypes needs to be investigated. A positive genetic correlation between seed weight and flowering time indicating that late flowering plants produce large seeds was found in *G. wightii* (Wutoh et al. 1968a).

The finding that diploid strains have faster germination rates of about one day than tetraploids (Table 2 and Fig. 6) is unexpected. However, mean percentage of germination for all tetraploids seems to be slightly higher (about 2%) than that for all diploids, especially at pH's 5, 7 and 8. Since tetraploids are probably more common in countries with high altitudes, e.g. Malawi and Uganda, and high latitude, e.g. South Africa (Edye et al. 1970), it is then possible to speculate that such places may have better drainage and possibly less soil acidity. In addition, such countries are relatively cooler which will produce strains with longer germination time than countries with relatively higher temperatures. Also, if, as suggested by Soliman (1976) and proven by Stølen and Andersen (1978), pH is independently under the control of few genes, it is then possible that such strains could be more homozygous for pH genes than diploid strains. Also, if they are originated by autotetraploidy then the doubling of genetic material might not have any profound effect on sensitivity to pH. However, there is a wide range of overlap between diploid and tetraploid strains (Fig. 2a and b; 3a and b) which allows for the utilization of pH-specific tetraploids (strain 1) in breeding programs for desirable agronomic characters (Hutton 1965).

In this experiment it was not possible to detect a lower

Table 2. Effect of ploidy on germination and seed weight in *Glycine wightii*

Ploidy		Percent Germination				Germination time (days)				Weight of 100 seeds (G)
		pH level				pH level				
		5	6	7	8	5	6	7	8	
Diploid	$\bar{x}$	40.44	41.89	40.44	38.33	3.83	3.49	3.45	3.48	4.868
(2N = 22)	SE	5.14	5.72	6.07	5.99	0.46	0.40	0.40	0.43	0.159
Tetraploid	$\bar{x}$	43.39	41.72	42.11	40.28	4.90	4.77	4.68	4.88	5.067
(4N = 44)	SE	4.00	4.53	4.00	4.30	0.33	0.26	0.33	0.36	0.214
t-value (df = 25)		0.438	0.022	0.235	0.263	1.683	2.750[a]	2.221[a]	2.369[a]	0.612

Means are based on 9 diploid and 18 tetraploid strains
[a] $P > 0.05$

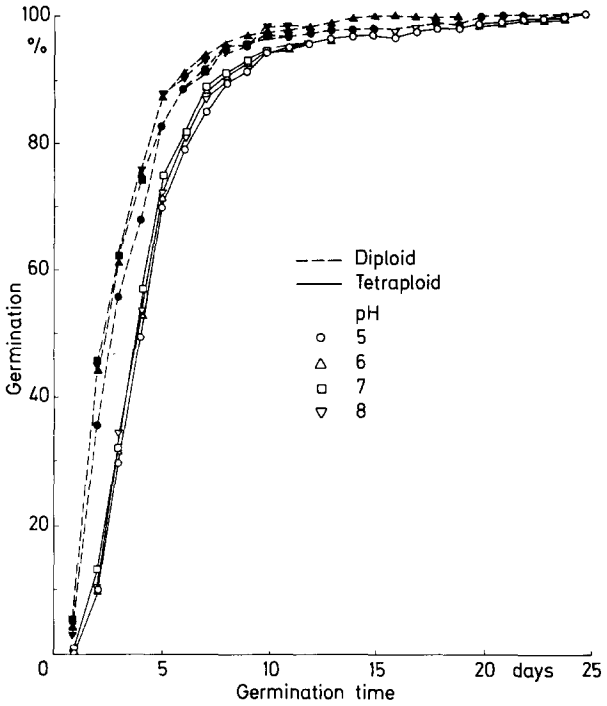


Fig. 6. Germination curves of *Glycine wightii* diploid and tetraploid strains at various pH levels

or upper limit of tolerance. This may be due to the small range of pH (5-8) which was initially intended and the gradual narrowing of this range (Fig. 1) through time. However, most of the strains showed a high degree of stability over the studied range. The nutrient media were not renewed during the experiment. If the media were renewed at frequent intervals a more stable range could have been obtained. It is expected that plants and hydrogen ion concentrations of their growth media have a reciprocal effect upon one another (Small 1946). Also, the use of buffered and unbuffered cultures may have different effects on germination and growth (McLay 1976).

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