CERTAIN ASPECTS OF THE BIOLOGY OF WATSONIA SPP.

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SUMMARY

The flowering responses of two species of Watsonia (*W. humilis and W. tabularis*) were studied both in the field and in the laboratory. There was no conclusive evidence that heat treatments directly influenced the flowering response. Instead, it appears that flowering may result from a number of factors such as watering, clearing the soil surface of vegetation and transplantation. The effects of temperature on seed germination were also investigated. 15 - 18° are the optimum temperature conditions for germination although viability is not affected by incubation at temperatures up to 35°C.

Carbohydrates in the form of mucilaginous polysaccharides are the major storage reserves of the corms. These polysaccharides as well as the ethanol soluble carbohydrates were determined at different stages in the life cycle of *Watsonia spp*. by means of gas-liquid and paper chromatography. There was little variation in the levels of cold water soluble polysaccharide at different stages in the vegetative development of the corms, but during seed pod formation the monomer components of these polysaccharides declined. The implications of these results are discussed in relation to the ecology of both *W. tabularis* and *W. humilis*.

1. INTRODUCTION

Considerable interest has developed with reference to increased flowering response of particular geophytes to veld fires in the Western Cape (Marloth 1908, Michel 1922, Adamson 1929, Hall 1959). Michell (1922) gave an account of profuse flowering of Haemanthus coccineus L. about one month after a fire on the slopes of Signal Hill, Cape Town, but during the following years the flowering response decreased dramatically. Oxalis spp. and many monocotyledonous plants flowered profusely soon after the fire, but their vigour and flowering response declined progressively during successive years.

Veld-fires in the Cape Province have probably been of regular occurrence since prehistoric times. Sim (1907) cited Vasco da Gama as having called the Cape "Terra de Fume" in 1497, due to the grey pall of smoke which hung over the area. At this time the veld was frequently burnt by the Hottentots, who probably followed this practice through centuries. The fire would remove the unpalatable dry grass and soon afterwards freshly sprouting shoots would attract game to the area and also provide pasture for cattle. The new grass regenerated from underground suckers and in the case of Andropogon hirtus on Signal Hill it only took two weeks for it to reappear (Levyns 1924). As a result of these observations European settlers in the Cape adopted this practice of veld-burning. The early settlers also believed the ash of burnt vegetation acted as fertiliser promoting the sprouting of fresh grass. (Kolbe 1792). The practice of veld-burning became very common, and a law was passed in 1687 (Botha 1924) which gave the death penalty to second offenders who were caught setting the veld alight. This law indicates just how serious the problem of uncontrolled veld-burning was in those days. However, even without man's help it is very likely that natural veld-fires in the Cape were a common occurrence. Wicht (1945) quotes incidents of sliding rock and lightning igniting the veld. During the Ceres earthquakes sliding rocks were thought responsible for igniting several spontaneous fires in the mountains. Troops of baboons also regularly dislodge rocks on mountain slopes and so may well be instrumental in causing fires. Thunderstorms are now infrequent in the Cape Peninsula and environs, but they may have been common in the Cape Province during times when the vegetation was more luxurious than at present (Botha 1924, Philips 1930). Fire at that time probably consumed far greater areas than the relatively small fires of modern times. Wicht (1945) describes the Great Fire of 1869, in which an area of 400 miles by 15 to 150 miles was destroyed. At present fires of this magnitude are unlikely to occur, as firebelts and modern fire-fighting techniques would tend to localise them.

It was only in 1962 (Bean 1962) that a specific study was made on the effects of fire on particular species of geophytes. Other studies (Levyns 1966, Martin 1966, Taylor 1973) had mainly been of a descriptive nature, with very few quantitative records (Hall 1959). Levyns (1966) described a disastrous fire which laid waste a large area of sloping ground between Betty's Bay and Rooi Els. This occurred during late December, when the vegetation was exceedingly dry. Two months later wonderful displays of *Kniphofia uvaria* (L.) Hook. f. (Red Hot Poker) were observed. Not far from Rooi Els a population of *Haemanthus canaliculatus* Levyns was also observed to be in full bloom. Another fire, Christmas 1965, resulted in striking floral displays of Red Hot Poker and *H. canaliculatus* two months later. After examining herbarium material Levyns concluded that fire definitely triggered flowering in H. canaliculatus.

A more active flowering response has been reported after fire for Cyrtanthus contractus N.E. Br. by Martin, (I966). On August I5th during a severe drought in the Grahamstown Nature Reserve, extremely dry heath vegetation was burnt. Despite the drought the first bulbs of C. contractus came into bloom only I5 days later, with the flowering head being pushed out of the ground on a short peduncle and the flower buds opening almost immediately. Only after flowering had stopped were the leaves produced. A similar response was reported for the geophyte Bobartia burchellii Baker. This plant also flowered profusely after a fire but subsequently only infrequently. Speculating on this "stimulus-response relationship", Martin suggested it was not perhaps so much the actual heat stimulus from a fire but rather the change in the daily temperature cycle that activated the bulbs. In experimental plots in which the temperature was monitored by sunken thermometers, Martin found the following maximum temperature differences:

Aug. I8th	Burnt Plot	Regenerating Heath	Unburnt Plot
I" depth	I4,5°	I2,0°	II,0°
4" depth	I2,0°	IO.0°	IO,5°
min.temp.	7,0°	-	8,0°

Obviously, on the burnt plot there were greater daily temperature fluctuations than on the unburnt ones. The explanation given for this is that "vegetation cover decreases the heat flow and therefore dampens fluctuations of this sort". The difference between temperature maxima of burnt and unburnt plots at the time, winter, were less than 2° at 4" depth. During summer the temperature cycle on burnt and unburnt plots amounted to 6 - 7° on the burnt and 3,5 - 5° on the unburnt plots per day. Martin (I966) also noted a "close similarity between the effects of burning and clearing", (i.e. the clearing of vegetation above ground level), with respect to the flowering response of certain plants. Therefore it appears that the removal of vegetation may be the stimulant for the flowering of certain species, rather than a stimulation by fire.

Whilst working on orchids in the Muizenberg Mountains, Hall (1959) found a definite relationship between the flowering of certain species of orchids and veld-fires. The very common <u>Satyrium bicorne</u> (L.) Thg. was found to be flowering mainly within the first year after a fire, the relative frequency being 80 plants or flowering colonies per square ¼ mile. In areas which had not been ravaged by fire during the previous 2 - 10 years the relative frequency had dropped to 7,5. Similarly, for <u>Pterygodium catholicum</u> (L.) Swartz, the relative frequencies for flowering were 17 soon after a fire and 2 in areas unburnt for 2 - 10 years. Also, in an area unburnt for at least 10 years, no flowering orchids at all could be found. However, in closely similar veld alongside this, which had been burnt 1½ years previously, eight different species of orchids were recorded as being in full bloom. In <u>Disa obtusa</u> Lindl. and <u>Orthopentea bivalvata</u> (L.f.) Rolfe, many more plants were observed to flower during the second season after a fire, but during the fourth season no dormant tubers could be found at the staked sites. This was surprising, as nearby on a firebelt burnt two years previous, many specimens of the above species were seen to be in full bloom. There was no clear explanation as to whether the enhanced flowering after fire was due to a direct stimulation of vegetative tubers at the time of the fire, or whether post-burn conditions were particularly suitable for the germination of windborne seeds. With respect to <u>Disa obtusa</u> and <u>O. bivalvata</u> the latter explanation is more plausible, as no dormant tubers of these species were found in the ground during the fourth season after a fire.

In a six-year study after fire on the western slopes of Table Mountain, Adamson (1935) recorded a definite increase in the numbers of geophytes. He compared this with geophytes found in the macchia of Corsica, where, even though there are fewer species than in the Western Cape Province, geophytes appear to flourish, forming crowded communities (Ruebel 1930).

Bean (1962) showed that certain Watsonia hybrids which had been burnt over in the field, produced over three times as many flowering spikes as did the unburnt controls. Compared with "unburnt" plants, however, the average number of flowers per "burnt" spike decrease. Nevertheless, the total yield of flowers from "burnt" plants was significantly greater than that from "unburnt" controls. In another experiment, Bean planted Watsonia hybrid corms in plots which were:

1. Cleared, then mulched with weeds.
2. Left cleared.
3. Left cleared, then fertilised with KCl fertiliser.
4. " " " " " woodash.

These treatments were repeated on two sets of plots whose previous history had been:

a. Unburnt, used as Watsonia beds for 8 years.
b. Burnt, after use as Watsonia bed for 8 years.

The only significant results from this experiment were that the mean lengths of flowering spikes from the burnt plot were approximately 12 cm. longer than those from the unburnt plots (1% level of significance). Also, the mean number of flowering spikes on burnt plots increased (5% level of significance). More interesting is the fact that all material had received an accidental veld-fire prior to lifting of the corms, with heavy rain washing the ashes from the fire deep into the ground afterwards. Therefore, despite this fire treatment, there were still significant differences in the flowering response, depending on whether the corms were replanted into "burnt" or "unburnt" soil. Clearly it is not only the direct heating effect of the veld-fire upon the soil and the corms which is operative, but also the cumulative and indirect effect of the heat-treated or burnt soil on the plant itself, as mere addition of woodash to the soil did not result in an increased flowering response.

Taylor (1973) mentions fynbos plants exuding poisons from their roots, these chemicals thereby altering the soil environment. In old stands of well-established plants this effect would naturally be most pronounced. If it is correct that fire is able to destroy the effect of these plant poisons, as Hanes (Taylor 1973) has postulated, then it is not difficult to explain the outcome of Bean's experiment.

Unfortunately the effects of fire on the soil are manifold. Both Bauer (1936) and Sampson (1944) found that burnt chapparal vegetation in the Santa Monica Mountains, Calif., held more moisture at depths greater than 6 - 9" than unburnt chapparal, during the dry season. They ascribed this to decreased transpiration, as all aerial plant parts had been destroyed during the fires. The surviving underground organs of geophytes are ideally suited to such conditions, and rapid growth and flowering is possible. In South Africa, Wicht (1946) found that much growth from underground organs did in fact take place after fires on experimental plots. Much of this growth took place during a very dry summer season. Wicht also found increased moisture levels under burnt vegetation, but he did not find these results statistically conclusive due to small sample numbers which were used. He did, however, consider Bauer and Sampson's work in the floristically similar chapparal vegetation of California to be indicative of similar conditions in the Western Cape Province.

Wicht found that on plots burnt sequentially every month from January to April, germination of seeds and the development of geophytes appeared to be neither promoted nor retarded during the first winter, but flower initiation of Oxalis spp. appeared to be promoted by a mid-summer fire. This agrees with Michell's results of 1922.

Outside South Africa much work has been undertaken on the stimulation of flowering in bulb and corm producing plants as a result of temperature treatments. However, the work was often undertaken from a commercial point of view, and has concentrated on plants of horticultural interest, e.g. tulips, dahlias, gladioli and hyacinths. Much of the published literature is difficult to obtain as it has been published in the lesser distributed bulletins of agricultural experimental stations. Very few of the South African geophytes have been studied under normal field conditions. The requirements to promote flowering, using standard gardening techniques, are well known for several examples. In Watsonia spp. the corms are normally lifted and divided at the end of the growing season. They may then be stored for a while under cool conditions before replanting. The leaves generally have died back before lifting and often are removed together with the old leaf bases which from a tough thick covering around the corms. Planting is done during autumn or spring, but in the case of evergreen Watsonias like W. tabularis the corms are not lifted annually. After replanting new leaves sprout from the apical bud on top of the corm and a new corm also starts to form through the swelling of the internodes of the developing leaves. The old corm shrinks at this time and is pushed down into the ground by the newly developing corm. Contractile roots from the new corm aid in pulling the corm down on top of the old one and at the end of the growing season all that is left of the old corm is a flat fibrous disc. On well established plants as many as eight such discs can be counted in the field. The flowers are usually initiated at the time the new corm develops, so that liberal watering is essential to produce good blooms later in the year. Sometimes more than one flowering spike is produced by a plant. This generally occurs when the apical bud has been damaged by fire.

Instead of being formed in the axil of a leaf near the apical bud, several spikes form in the axils of leaves further down on the corm. Vegetative reproduction of the corms also occurs from lateral buds. Several corms are then initiated simultaneously. The swelling of the new corms pushes them apart, so that after several seasons the corms are distinctly separate, forming a small cluster of plants.

The development of corms of the gladiolus is similar to that of watsonia. After planting, flower primordia begin forming within six to eight weeks, although primordial initiation may be delayed by cooler weather. When the corms are lifted they appear to be in a state of deep rest which disappears slowly at 20 - 30°, but the process can be accelerated to occur in only 3 - 6 weeks if the corms receive a low temperature treatment of 3 - 10° (Denny, 1936). Tavernetti and Emsweller (1934) found that they were able to accelerate flowering by 2 - 6 weeks by heating the soil to 15 - 21° for two months. In Palestine two crops may be grown in one year with the winter corms developing immediately after replanting and the summergrown corms requiring cold treatment of 4° for 20 days to break their rest period. (Evanari, Konis and Zirken, 1950). It has also been suggested that the dormancy of Gladiolus sp. buds may be induced by high summer temperatures (Ryan, 1955). Photo-period and light intensity may play a part. Pfeiffer (1931) showed that Gladiolus sp. flower spikes stopped growth in winter,(termed "blasting"), and he attributed this "blasting" to an insufficiency of light. Jones and Loomis (1930 and 1934) respectively have shown that "blasting" could be almost completely overcome by providing additional winter light. It appears however, that light intensity and not duration is the factor preventing "blasting" (Loomis, 1934).

Freesias are also indigenous to South Africa and flower initiation commences soon after the corms have been planted. In Europe this is usually done during September and October.

Corms which have been stored during summer at 9 - I7° may fail to sprout and may only produce vegetative parts, but storing at the higher temperatures induces rapid sprouting in the Freesia varieties "Daffodil" and "Buttercup" (Hartsema and Luyten, I939, I944). Corms of the "Buttercup" variety can be induced to flower earlier by storing for I0 weeks at 3I°, followed by 4 weeks at I3°. Under such conditions plants will flower in November. If the initial storage temperature is reduced to 25½°, some of the plants may become "sleepers", i.e. producing no flowers at all during that season.

Immediately after lifting of *Gladiolus*, *Watsonia* and *Freesia spp*. corms there is a definite dormant period whereas in the tulip there is a period of "after-ripening". When, as in Europe, tulip bulbs are lifted in early July, all aerial parts have died down. The bulbs are then stored dry for about three months while the growing point inside the bulb remains active. During this time the one or two rudimentary foliage leaves which were present at the time of lifting have increased up to five in number by the initiation of new leaves. The floral buds are also initiated quite soon, so that by early September all floral parts are preformed. The flowers however, do not come into bloom until spring, i.e. April or May of the following year. The new bulb develops at the same time as the roots, which start forming very slowly during October.

Amaryllis belladonna has been studied in the Netherlands and is also indigenous to the Cape. Flower initiation begins during August. The assimilating leaves die back during early summer of the following year and suddenly in September the inflorescence emerges, followed by a number of vegetative leaves. In the Cape flowering also occurs after the warm summer months, particularly so after a fire (Adamson and Salter. I950). However, it is not known when flower initiation of this species occurs in the Cape.

In general, higher temperatures appear to promote flowering in corm and bulb producing plants, as is shown by the optima for different species: Tulipa sp. 7-20°, Amaryllis sp. 23°, Hyacinthus sp. 25,5°, Lilium sp. 23°, (Hartsema, 1961) and Freesia sp. 31°. With Gladiolus sp. 30-35° was found to be optimal (Volz and Keyes, 1935), but Denny (1936) showed that a 3-10° incubation before heat-treatment could shorten the rest period. This treatment had to be given before the "deep rest" of the corms had disappeared. In the case of Volz and Keyes' work this "deep rest" had already been broken before the treatment. It appears as if the corms are in an innate state of dormancy for a short time after the growing season has ended, and the aerial parts have died down. Thereafter they remain in a quiescent state, only waiting for a climatic "trigger" to activate growth.

In Convallaria sp. the deep rest can be broken by a -5 to -2° treatment, in Lilium sp. this will occur at 7-10° (Hartsema, 1961). Lower temperatures also stimulate extension growth. Hartsema (1961) showed that temperature treatments provide extension growth resulting in early flowering of tulips, hyacinths, daffodil and iris. All these species had temperature treatment optima around 7-13°. Work by Algera and Rodrigues Pereira, quoted by Hartsema (1961), showed that low temperatures were required for the mobilization of stored food substances.

In this thesis corms of two species of Watsonia will be studied in relation to the levels of storage products and their utilization during growth and development of the plant. Small corms provide ideal experimental material and can be obtained from genetically uniform population in the field. The terminal bud, being sub-terranean, is protected from light and flower initiation can proceed away from the inter-action of light-dependent processes. In the small cormed W. humilis Mill. these considerations apply, but as flower formation occurs concommitantly with the development of leaves, it is difficult to explain the influence of various factors on each of these developments. However, an attempt will be made to show in which direction research on the fire-induced flowering of Watsonia spp. may be most rewarding.

2. MATERIALS

Experimental work was performed with two species of Watsonia. Large numbers of *Watsonia humilis* have been found after fire near the Cape of Good Hope Nature Reserve (Goldblatt, private communication). A search of the area during January only revealed a small number of this species but a large colony of *W. tabularis* was discovered. This Watsonia has larger corms than *W. humilis* but had shown periodic blooms of extraordinary proportions and for this reason was selected for further study. Later in the year a colony of *W. humilis* was discovered nearby.

Both colonies were growing in an uncultivated field or paddock on land owned by a Mr. O.T. Ryan of Hillside Poultry Farm, Kommetjie Rd. Klaasjagers. The land lies on slightly sloping ground between the Kommetjie Road and the Klaas Jagers stream, which runs along the foot of the Sweetvalley in a northwesterly direction (Cape 3418, Long. E $34^{\circ}15'$, Lat. S $18^{\circ}26'$). The *W. tabularis* colony grows in a belt about 50 x 10 m parallel to the Kommetjie road and about 30 m away from it to the East. Plant distribution is random with a density of about four plants m^{2}. Other dominant species are *Pteridium aquilinum* Kuhn and various restionaceaus plants, which are common throughout the area. Scrub cover is sparse and seldom exceeds 60 cm in height. This is probably due to the annual mowing, undertaken to improve the pastoral value of the land. Outside the experimental plots the land has been fertilised with chicken manure at 3 m intervals and has also been seeded with *Stenotaphrum secundatum* O. Kuntze.

Many Composite weeds have been introduced into the area. Cattle use the paddock infrequently and only once proved a nuisance by breaking of dried flowering spikes before all data had been collected. More serious was the damage caused by caterpillars of the Pine Emperor Moth to plants of W. tabularis. Some plants suffered leaf area reductions up to 90% due to grazing by the 6-I3 cm long caterpillars. Dune-rats are common in the area but do not appear to damage W. tabularis corms under natural conditions. However, corms of W. humilis are eagerly sought after by them and at one stage it appeared as if the whole of the W. humilis colony might succumb to them.

This W. humilis colony is found only I0 m West of the Klaas Jagers stream. W. humilis plants are smaller than those of W. tabularis and the corms only weigh between 3-30 g as opposed to 60-500g for plants of W. tabularis. W. humilis grows in small aggregates of 5-50 plants, the plants sometimes being so crowded to virtually exclude all other species. The topography of the site is generally flat, some areas being raised about a foot above the surrounding land. These higher areas are densely overgrown with pteridium and also some W. tabularis. The latter is however not as vigorous as on the main site. During winter the water table is very close to the soil surface. The species distribution is slightly different here as opposed to the other site; reeds, grasses and small herbs being more common here. The colony is partly surrounded by dense Acacia cyclops Cunn. and A. cyanophylla Lindl., which extends all along the riverbank in a dense community. The proximity and highly inflammable nature of this bush made experimental burning impossible on this site. On the W. tabularis site burning could be undertaken with a fair degree of safety.

The soil on both sites is a fine grey sand derived from the weathering of Table Mountain sandstone. On the upper W. tabularis site the soil is dry to a depth of 30 cm during summer, but on the lower W. humilis site, only the upper I5 cm appear to have a low moisture level. This site is in close proximity to the water table. There also is an apparently greater accumulation of organic matter on the lower site.

However, the evergreen W. tabularis plants on the upper site do not seem to be suffering from a lack of water during summer. This may be due to the fact that their roots are able to reach a subterranean seepage area, fed from the higher lying rocky ground on the southern side of the Kommetjie road.

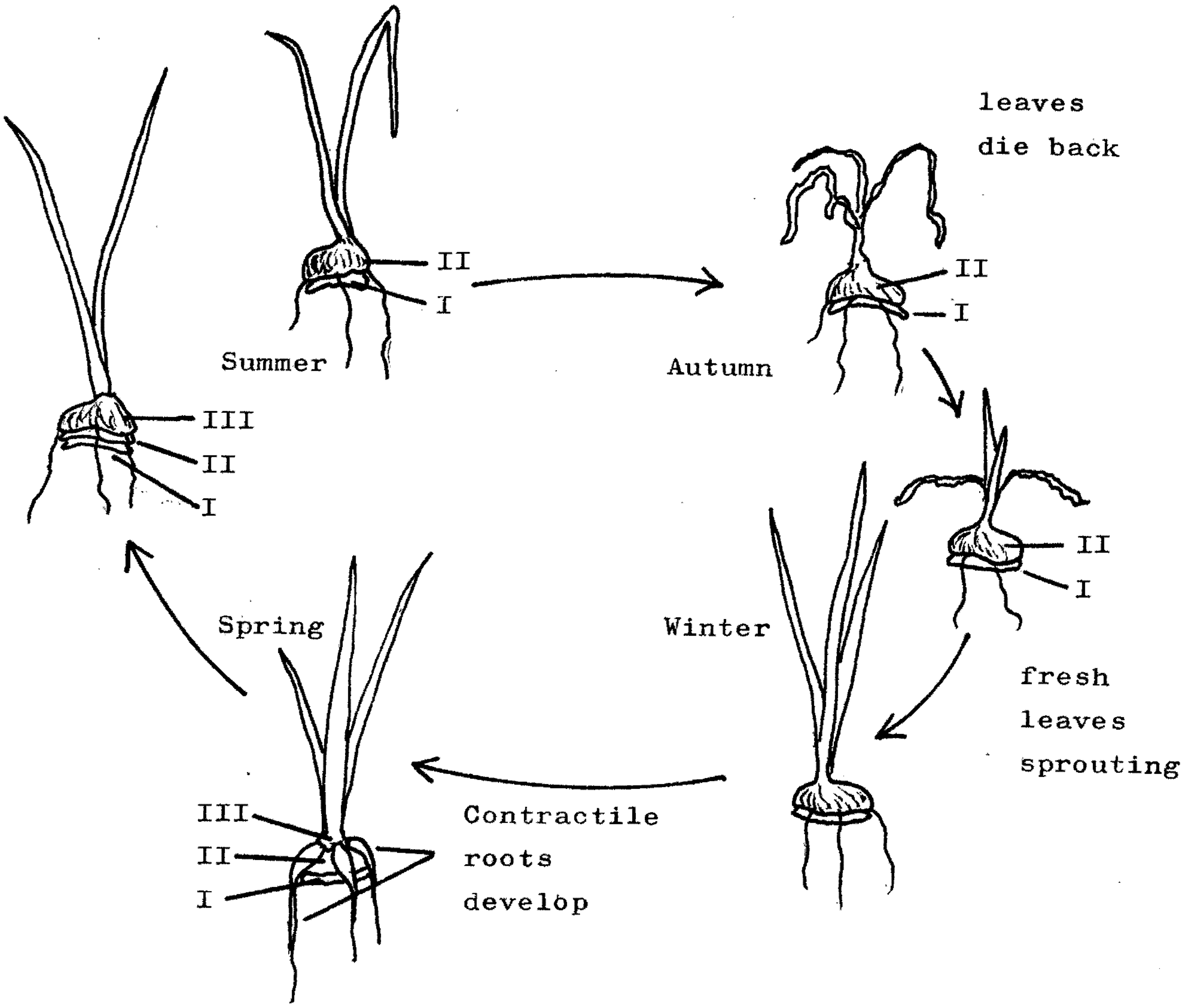
3. SEASONAL CHANGES IN CORM WATER CONTENT

The long dry summers experienced in part of the winter rainfall areas of the Western Cape cause many plants to suffer from acute water shortages during the dry season. Many Watsonia spp., amongst them W. humilis, lose their leaves then and appear to suffer under drought conditions. South African garden manuals (Eliovson, 1968) stress the importance of proper watering regimes to promote flowering in Watsonia spp., and water availability clearly plays a major role in the biology of these geophytes. To obtain data on the water levels present in corms, samples were collected in the field and fresh and dry weight determinations were undertaken in the laboratory. This was usually done within two hours after collection, the corms being initially stored in polythene bags. Corms were weighed after removing all roots and "discs" of old corms adhering below the current or "new" corm. After sectioning and removal of material for chemical analysis the remains of the corms were again weighed, then dried at 95°C and finally stored in a dessicator. They were then weighed to obtain the dry weight. Leaves were treated similarly. To obtain a true picture of leaf water content under actual field conditions during the day, leaves were cut off the plants in the field and immediately sealed in polythene bags to prevent any change in the leaf water content.

The water content of W. humilis was determined at about monthly intervals throughout one annual growth cycle. The successively older corms on a plant were identified by numbering them from I to III, as is shown in figure 1.

Fluctuations in the moisture content of W. humilis corms at varying stages during their development are shown in figures 2 and 3. Corm numbering is identical to that used in figure I.

Figure I. Development of W. humilis corms.



It appears that in an active "current" or "mature" corm (II), the water content is correlated with the wet season, being greatest in winter. As the corm becomes "senescent" and is compressed into a flat disc-like "old corm", the moisture content increases again. In the "old" corm (I) the dry weight progressively decreases but appears to reach a fairly stable low value late in the year. The developing new

Figure 2. Seasonal moisture content and dry weight of mature (II) and developing (III) W. humilis corms.

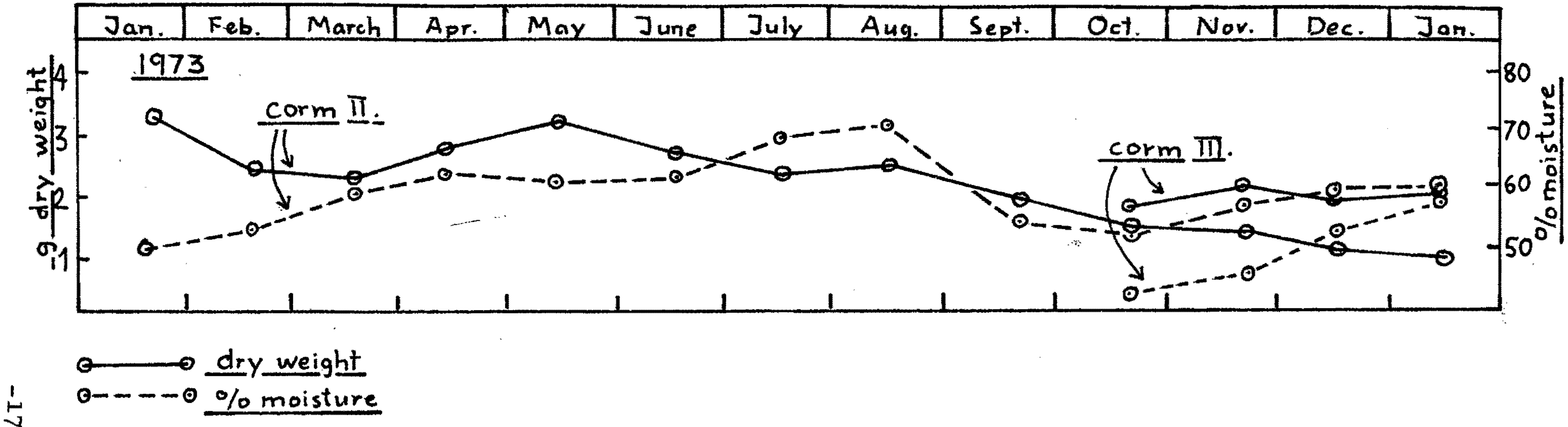
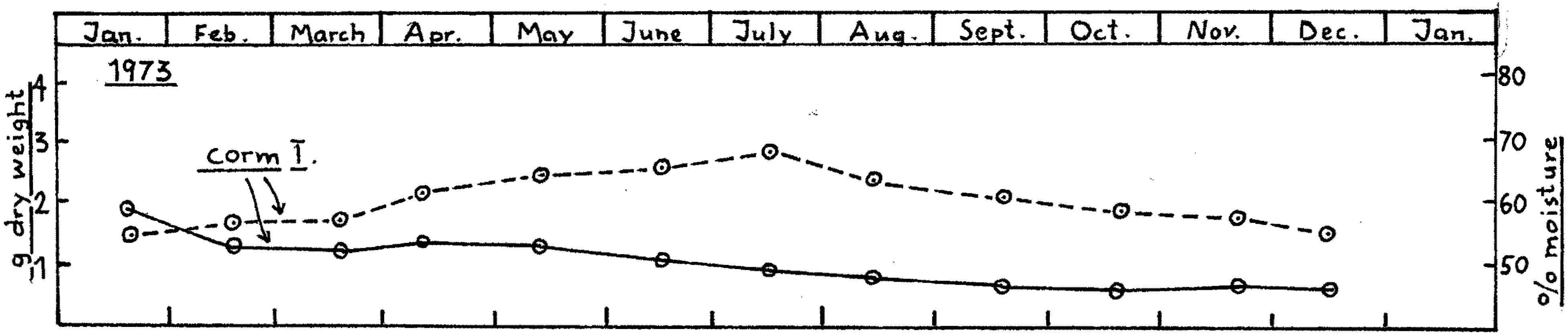


Figure 3. Seasonal moisture content and dry weight of moribund (I) W. humilis corms.



corms (III) rapidly increase in weight while the moisture content remains at a relatively high and constant value.

The dry weights of developing corms appear to be strongly influenced by the prevailing weather conditions. From figure 2 it is seen that during January of 1973 and 1974 the developing corms show widely differing values in dry weight, but according to the sampling dates both 1973 and 1974 corms should be in a similar state of development. Moisture levels in W. tabularis corms were not monitored as regularly as in W. humilis. However an appreciable difference in the moisture levels of corms from flowering plants growing on burnt ground as compared to non-flowering plants growing on unburnt ground was estimated. This difference was most pronounced during late summer, i.e. the dry season and disappeared with the onset of autumn.

Table 1. Water content of W. tabularis corms growing on burnt and unburnt ground.

Date	percentage moisture	
	non-flowering, unburnt	flowering, burnt
25-12-72	68%	72%
18- 2-73	56%	69%
12- 4-73	76%	79%
11- 5-73	74,6%	75,9%
19- 9-73	79%	81%

4. TEMPERATURE EFFECTS ON CORM DEVELOPMENT AND SEED GERMINATION

Fire in vegetation has an initial short and direct temperature effect on geophytes and also imposes a subsequent temperature regime through exposure of the bare soil to insolation. This results in marked temperature cycles during day and night. Vernalisation experiments have shown that plants are susceptible to temperature treatment, and it could be possible that the solar heating effect alone on certain geophytes could be directly responsible for flowering in certain species. An attempt was made to study temperature effects on corms of W. tabularis and W. humilis both in the field and through heat treatments applied in the laboratory. Seed germination was also studied under different temperature regimes in the laboratory and the results of all these studies were correlated to the ecology of these plants.

Field experiments.

1. Surface treatments

The effect of fire, clearing, clearing together with the application of woodash, and simple mulching were studied on single plots of W. tabularis. The 25 m^2 plots were staked out in line in a dense colony of W. tabularis, so that each plot contained 100 to 120 plants. Each plot was allowed to overlap 30 cm into the veld, so that edge effects were minimised. The plots were then treated on 24-3-'72 as shown below.

Plot 1. Control, left untouched.
" 2. Burnt during early morning but the vegetation was very dry. Some additional fuel was added in the form of dry grass clippings left over from the last cutting of the field. A light breeze fanned the flames and the fire burnt fiercely for only 30 min.

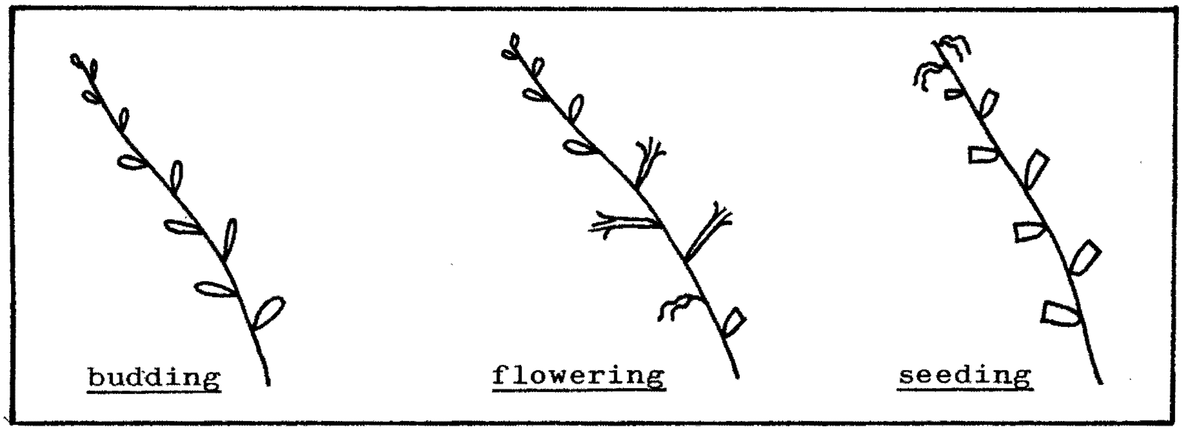
Plot 3. Cleared of highly inflammable vegetation so as not to be a fire hazard during the burning of plot 2. Ashes collected from a veld-fire spread over the plot at a rate judged to be similar to what would have been obtained if the plot had been burnt itself. The removed vegetation was not replaced however.

" 4. Vegetation other than *W. tabularis* was cleared above ground level only. Organic detritus and leaf remains were removed as far as possible, giving the plot the appearance of a freshly cut firebelt, with the soil completely exposed to the sun.

" 5. The vegetation removed from plot 4 was spread around the bases of *W. tabularis* plants and augmented with clippings from other areas. All the original vegetation was left standing.

The growth and development of these plants was observed for two years. The number of offsets produced and the number of flowers per offset, as well as the dates on which the flowers came into flower, were recorded. In watsonias flowering proceeds acropetally, with the result that one particular spike may contain buds, open flowers and developing seed capsules simultaneously. Any particular spike was judged to be in a"budding" stage when no flowers had yet opened; when flowers on it had opened it was termed to be "flowering" and if all flowering had ceased it was termed "seeding".

Figure 4. The changes in development of flowering spikes of *W. tabularis*.



The plants came into flower about nine months after the treatments, when the following data was collected:

Results.

Table 2. Flowering results from experimental W. tabularis plots at the end of the first flowering season, Feb. 1973.

treatment	burnt	cleared, ashed	cleared	mulched	control
total plants	88	86	124	99	112
flowering %	56,0	46,5	55,0	32,4	59,0
spikes/plant	4,26	3,92	5,62	3,27	4,60
std. deviation	1,03	1,06	1,82	0,79	1,73
flowers/plants	77	61	72	57	76
std. deviation	28,9	17,3	21,0	15,1	23,7
flowers/spike	18,07	15,56	12,81	17,43	16,52

1) The mulching treatment significantly inhibited flowering. (chi-square test probability level better than 0,1) No significant difference in numbers of flowering plants were found between the remaining treatments.

2) The numbers of flowers produced per flowering mulched plant was significantly below the flower/plant ratio of the control plants. (P=0,02 - 0,05). The "ashed and cleaned" plot also showed decreased flower/plant ratios as compared to the control plot. ($P \cong 0,05$)

3) Flowering mulched plants showed significantly less offset production than flowering control plants. (P better than 0,02). The "ashed and cleared" plot showed a similar result.

4) With reference to figures 5-7 on the following pages it can be seen that the flowering process on the "cleared" plot was accelerated compared to all other treat-

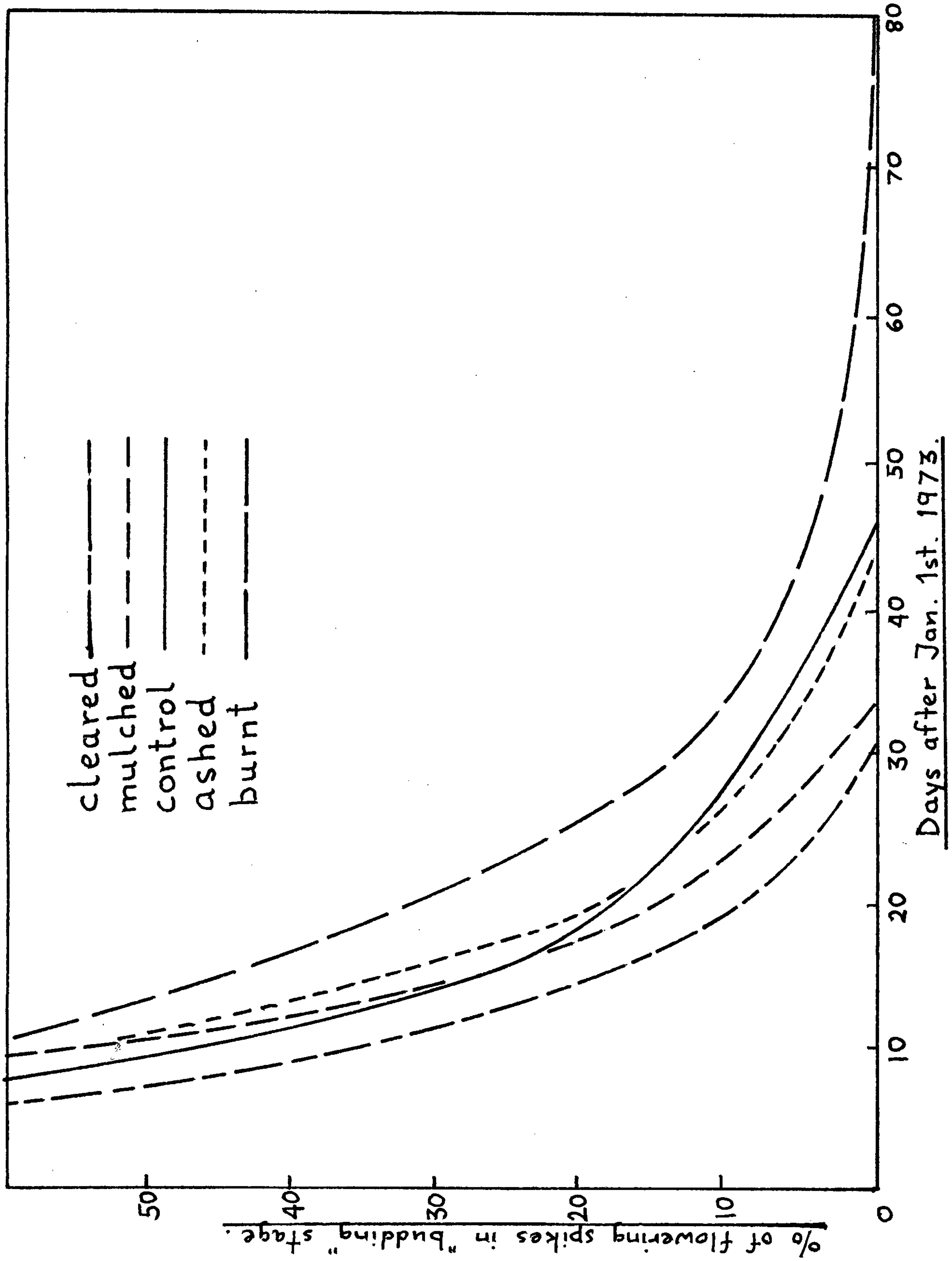


Fig. 5. % of spikes of W. tabularis in a"budding" stage on experimental plots.

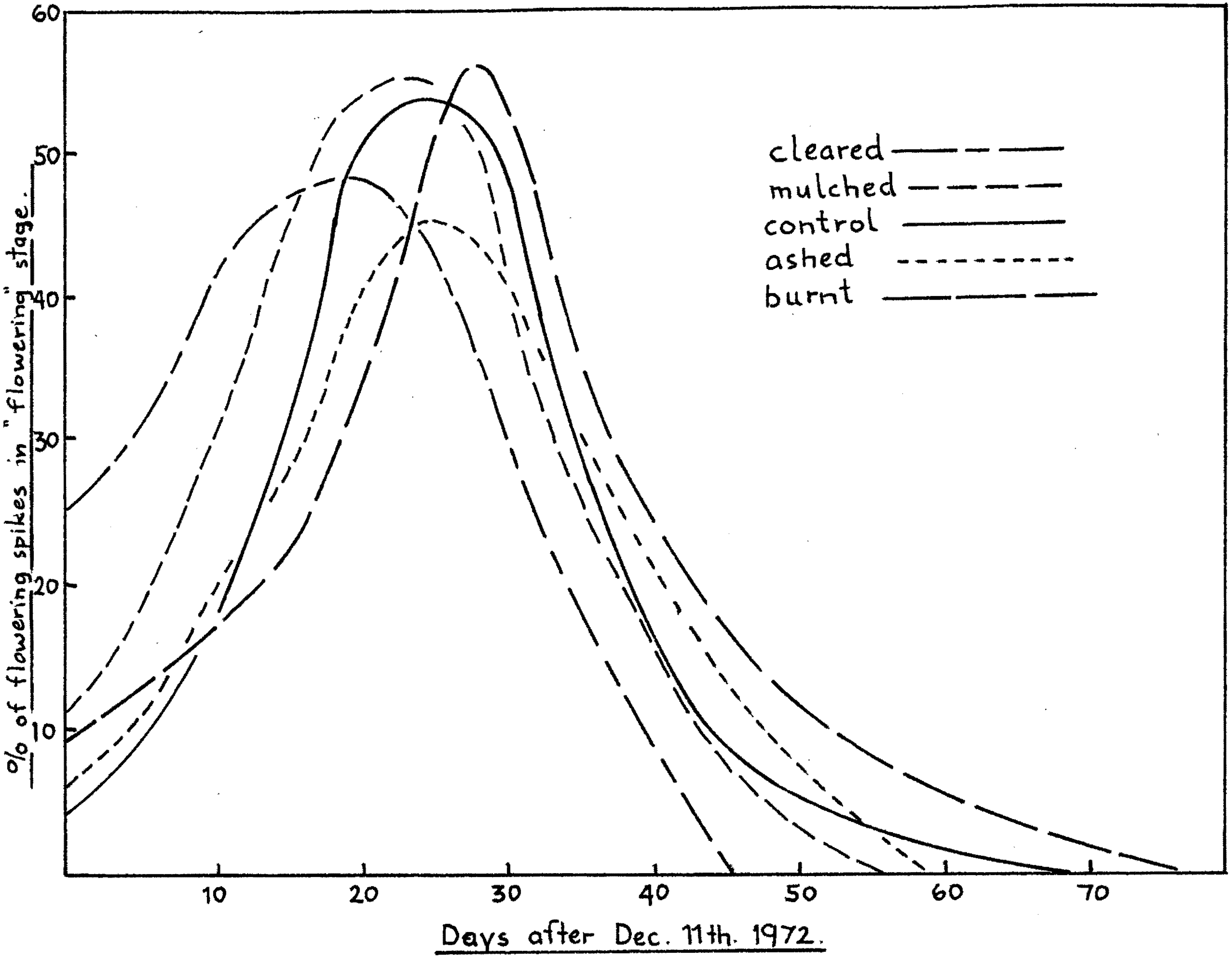


Fig. 6. % of spikes of W. tabularis in a "flowering" stage on experimental plots.

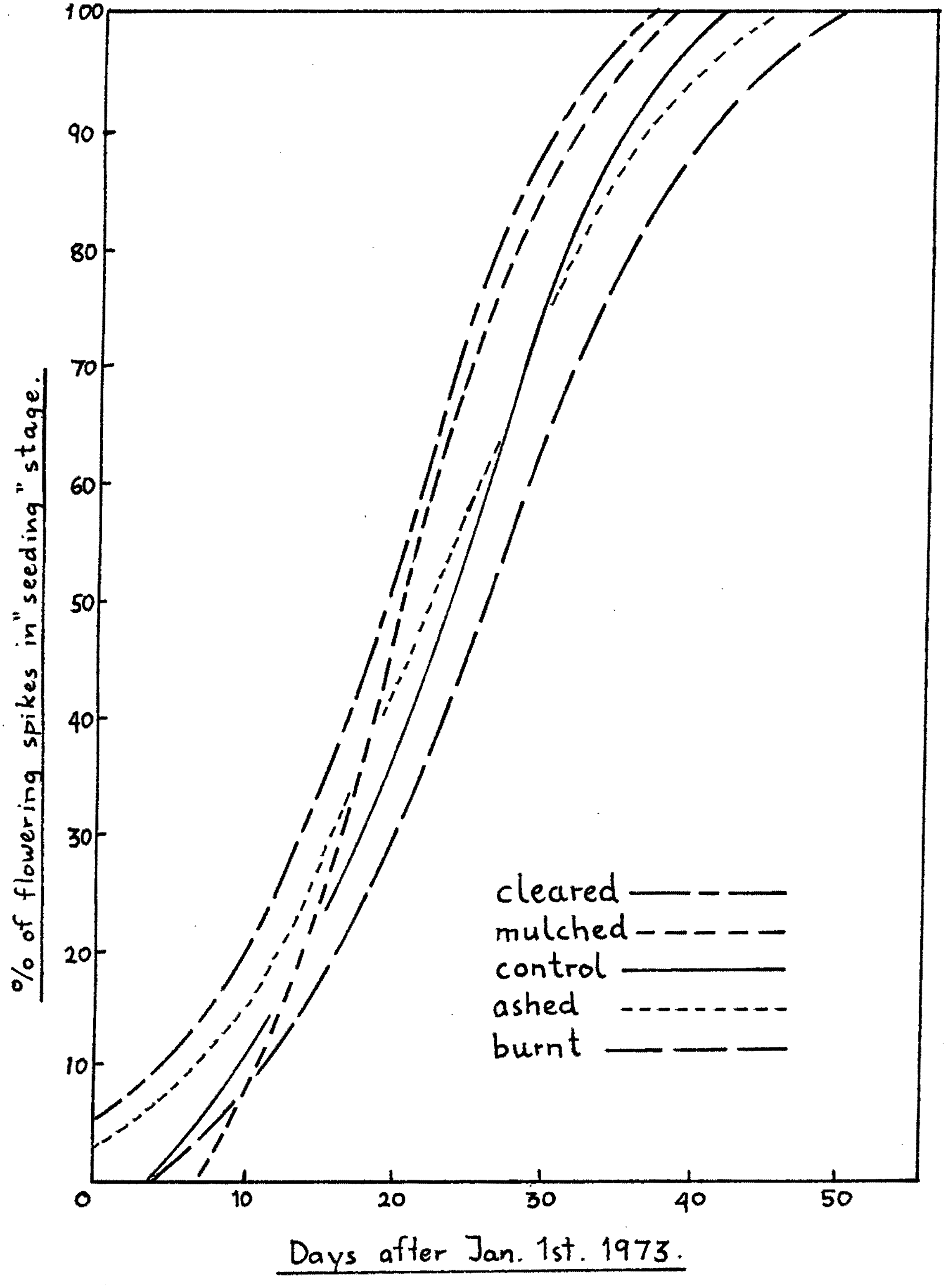


Fig. 7. % of spikes of W. tabularis in a "seeding" stage on experimental plots.

ments, while flowering on the "burnt" plot was retarded.

During the next flowering season (1973/74) the flowering plants were again counted on the plots. No further maintenance had been undertaken on the plots in the interim, so that the plots were regressing to their original condition. They had not been mown for two years and Pteridium sp. had become dominant in most plots. On the burnt plot Oxalis spp. and Geranium sp. were common, as well as Pteridium sp. which was regenerating from rhizomes. The watsonias appeared to be flourishing on all plots, despite the dominance of pteridium. On the "cleared" plot restionaceous plants appeared to be more successful in regenerating from underground organs than the pteridium. On this plot ground cover was markedly denser than on the "burnt" plot, but still much lighter than on the control. The "cleared and ashed" plot looked similar to the "cleared only" plot. Least plant growth appeared to have taken place on the mulched plot. The plants here all appeared to be less vigorous than on the other plots, and grass appeared to be most successful in penetrating the mulch.

Flowering on the plots was not observed during the 1973/74 flowering season, but data on the numbers of flowering plants was obtained from the fertile spikes present during February 1974. These spikes become hard and durable after ripening of the seed-pods and remain attached to the plants for at least six months after flowering has occurred. Table 3 compares the numbers of plants flowering in the 1972/73 season with those found flowering in the following season.

It is seen that during the 1973/74 flowering season a decrease in flowering response was recorded, while the numbers of plants in several plots appeared to have increased slightly. However, it is extremely difficult to count corm (=plant) numbers accurately by the pattern of foliage seen above ground. Burnt corms especially appear to be stimulated to sprout from several buds, possibly due to the frequent destruction of the apical bud in the heat of the fire and the apparent increase in corm numbers on the "burnt" plot two years after the fire may be due to over-estimation of the number of plants present. However, extra care was taken during the counting of the "burnt" plants as this phenomenon had been anticipated.

Table 3. *W. tabularis* plants flowering on experimental plots during 1972/73 and 1973/74.

treatment	burnt	ashed	cleared	mulched	control	season
total no. plants	88	86	124	99	112	1972/3
% flowering	56%	46,5%	55%	32,4%	59%	
total no. plants	103	89	121	108	113	1973/4
% flowering	8,7%	7,8%	5,8%	17,6%	9,7%	

2. Laboratory temperature treatments.

Corms of *W. tabularis* and *W. humilis* were subjected to short temperature treatments before they were transplanted. The subsequent growth and flowering responses were then recorded.

2.1. Treatments on *W. tabularis* corms.

Corms of *W. tabularis* were collected under cool and cloudy conditions on the morning of 3-3-1972. After a preliminary storage of three days in a cool dark cupboard they were treated. Immediately prior to treatment the aerial leaves as well as the old adhering corms and rootlets were removed from the corms. In certain instances the old fibrous leaf bases ensheathing the corms were also removed. In these completely denuded corms heat penetration during heat treatment is believed to be far more efficient than in corms well insulated by a thick coat of old fibrous leaf bases. Very bad heat penetration in uncleaned corms is indicated by experiments done by Bean (1962), which showed that some *Watsonia sp.*

corms were able to survive hot air treatments of 90-100°C for as long as 25 minutes.

Wet heat treatments: Corms were heated in a thermostatically controlled hot water bath at 50°C. After allowing for a short initial period of temperature adjustment the corms were kept in the bath at 50° for one hour.

Dry heat treatments: Corms were incubated in ventilated temperature controlled ovens, a short period being allowed for temperature adjustment before the start of timing the treatment. Treatments continued for one hour at 50°, the corms being spread over a perforated metal tray, so that adequate air circulation was ensured.

2.2. Planting of treated W. tabularis corms.

The heat-treated W. tabularis corms were planted into 20 X 20 X 40 cm long asbestos troughs, using a light gardening soil similar to that found in the natural habitat of the plants. The use of troughs was to enable the corms to be heat-treated in situ at a later date, and also to prevent damage to the corms by burrowing rodents. Corms were planted five or ten to a trough, the corms having been selected so that each trough contained corms of similar sizes. (see table 4) Several of the troughs were provided with a mulch of expanded vermiculite chips, scattered over the soil surface to a depth of about 6 cm. Two windbreaks, to shelter the plants against the south-east wind, were also erected. These sheltered the plants in the absence of natural vegetation. To record sub-soil temperatures, thermometers were buried vertically amongst the plants at varying depths. The troughs were buried in soil up to the rims and watering was carried out every second day for two weeks. Thereafter water was given very sparingly, relying almost wholly on natural precipitation to sustain the plants' water needs.

In addition to the transplantation into troughs, the largest as well as the smallest untreated corms that had been collected, were planted directly into open ground in the University of Cape Town nursery. They received a watering regime similar to that of the treated corms and controls.

2.3 Results of heat treated *W. tabularis* corms.

Only two plants out of 150 heat treated *W. tabularis* plants and controls planted in troughs flowered during the (1972/3) current flowering season. Of thirty of the smallest-sized corms planted in open ground two flowered, and twenty of the largest corms, ranging in weight from 200-400 g each, produced four flowers. The percentage flowering obtained was far below that obtained on the experimental plots in the field.

Throughout 1973 a far more liberal watering regime was adopted, the plants being watered at least every two weeks during the dry season. Nevertheless only three medium-sized corms planted in troughs flowered. (see Table 4, troughs No. 5, 11 and 12). Of the smallest-sized corms planted in the open 27% flowered while 60% of the 20 largest-sized corms planted in the open flowered. The extremely poor flowering response of corms planted in troughs made statistical evaluation of the flowering response impossible.

However, leaf production of the corms planted in troughs had been recorded until late Nov. 1972. Leaf dieback occurred then and measurements were thus discontinued. Analysis of the leaf-lengths produced by the corms under various treatments indicated that mulch on the troughs tended to enhance leaf production. Leaf dieback in the mulched troughs appeared to be less severe as well, compared to non-mulched troughs. The mulching treatment produced significantly greater leaf production in the smaller corms. (see Table 4, troughs 3, 4, 7 and 8. $P=0,01 - 0,05$). Of the troughs containing the larger sized corms, only no's 11 and 12 showed similar increases in leaf production with the mulching treatment. (at a level of significance, $P\leq 0,05$).

Table 4. Average weight and leaf production of W. tabularis corms transplanted into troughs.

treatment, trough no.	no. corms.	∅ wt.g.	ratio: leaf length ÷ corm weight 25-11-'72.	no. of off-sets	signif. level
control +M 17	5	160	1,26	1	not
" -M 18	5	154	1,32	0	
" -M 11	10	151	1,73	0	>0,05
" +M 12	10	148	2,34	0	
" +M 5	5	109	1,96	0	>0,2
" -M 6	5	114	1,11	0	
" +M 8	10	60	2,14	0	>0,01
" -M 7	10	58	1,41	0	
WH +M 1	5	165	1,02	1	not
" -M 2	5	193	0,91	0	
" +M 3	10	60	1,43	0	>0,05
" -M 4	10	59	1,04	0	
" +M 13	10	147	1,61	1	not
" -M 14	10	144	1,99	2	
DH +M 9	10	161	1,23	1	not
" -M 10	10	159	1,70	1	
" -B-M 15	10	158	1,75	2	not
" +B+M 16	10	164	1,72	0	

Table 5. Analysis of treatments on W. tabularis planted in troughs.

Treatment, trough no.	Ø wt.g.	mean leaf length, cm.	n	s. dev.	Δ means	σ d	t	Signif. level
control -M 11	151	261	10	75	86	40,9	2,10	>0,05
" +M 12	148	347	10	105				
" -M 7	58	83	10	25	45	13,2	3,44	>0,01
" +M 8	60	128	10	33				
WH +M 3	60	123	8	34	36	15,3	2,35	>0,05
" -M 4	59	87	9	28				
control +M 5	109	213	5	54	56	30,5	1,84	>0,2
" -M 6	114	157	4	42				
control +M 8	60	128	10	33	5	16,1	0,31	
WH +M 3	60	123	8	34				
control -M 7	58	83	10	25	4	12,1	0,33	not signif.
WH -M 4	59	87	9	28				
DH +M 9	161	191	9	110	153	49,5	3,10	>0,01
control +M 12	148	347	10	105				
DH -M 10	159	237	8	106	24	44,3	0,55	not signif.
control -M 11	151	261	10	75				
DH -B-M 15	158	256	8	78	28	38,8	0,73	"
DH +B-M 16	164	274	9	81				
DH -B-M 15	158	256	8	78	91	42,9	2,11	>0,05
control+B-M 12	148	347	10	105	77	38,1	2,02	close 0,05
DH +B-M 16	164	270	9	78				

Wet heat treatment did not materially affect leaf production of small corms grown in troughs. Dry heat treated corms grown under mulch however showed a significant reduction in leaf length produced compared to an untreated control group. (troughs 9 and 12, P 0,01) The treated corms were, however, somewhat heavier on average than the control corms. Dry heat treated corms grown without mulch and without their protective sheathing of old fibrous leaf bases, showed leaf production comparable to dry heat treated non-mulch controls retaining their old fibrous leaf bases. Both dry heat treated groups of corms, either without or with a sheath of old leaf bases, produced less leaves than controls without a heat treatment. (troughs 12, 15 and 16. P 0,05)

2.4 Treatments on *W. humilis* corms.

W. humilis were collected in the field on 3-5-1973 and received various temperature treatments after a two-day storage period under cool and dark conditions. Out of approximately 350 corms collected only twenty had flowered around February, 1973. Both the largest and smallest corms were discarded and the remainder were sorted into batches of either 10 or 20 corms. Each batch was made up of corms of varying sizes, ranging in weight from 2-10 g each. All leaves were cut off the corms, the bulk of the corms having started sprouting new leaves. In some groups the "discs" of adhering corms were also removed.

Wet heat treatments: Groups of corms were stored in open paper bags in un-illuminated temperature controlled refrigerators and incubators at temperatures ranging from 0 - 35° for periods of one and two months. At the higher temperatures the corms tended to dessicate and distilled water was sprayed onto the corms at intervals of a few days. Despite this treatment corms stored at temperatures above 25° became noticeably lighter in weight than groups stored at below 15°C. The cooler temperature appeared to be less dessicating to the corms, possibly due to a higher relative humidity.

2.5. Results of temperature treating W. humilis corms.

With reference to figure 8 heat-treated corms in water at 40° for 4,8 and 16 hours, progressively delayed sprouting. Corms treated for 8 hours commenced sprouting after 13 days, while corms treated for 16 hours only started sprouting 44 days after the first sprouts of 4-hour treated corms had emerged. Once sprouting had begun in a group of corms, it progressed more rapidly in 16-hour heat-treated corms than in 4- or 8-hour heat-treated groups. This can be seen from the increasing slope of the graphs of figure 8, which shows slopes of 0,32; 0,43 and 0,48 : 1 respectively for the 4,8 and 16-hour heat treatments. Although there is a 1½ months' difference in the dates of first sprouting of 4 and 16-hour heat treated corms, both these groups sprouted under fairly similar cool and wet conditions prevailing during June and July of the Cape winter. Long low-temperature treatments also retarded sprouting, which is shown in Table 6.

Table 6. Sprouting behaviour of W. humilis corms stored at various temperatures for one and two months.

treatment	planted	1st sprout up: days after planting	days between 1st and last sprout up.
10°+oc 1 mth.	5-7-73	18	17
10°-oc 1 "		20	12
10°+oc 2 "	1-8-73	38	33
10°-oc 2 "		33	24
5°+oc 1 "	5-7-73	29	48
5°-oc 1 "		27	34
5°-oc 2 "	1-8-73	58	13
5°+oc 2 "		no sprouting	no sprouting
0°+oc 1 "	5-7-73	38	29
15-35° 1,2 "		no sprouting	no sprouting

oc = "old corms"

Both the duration of temperature treatment as well as the temperature used appear to control the onset of sprouting. In corms treated for one month, the onset of sprouting occurred at 18, 29 and 38 days after planting. The two-months treatment further delayed the onset of sprouting. Treatment at 0° for one month and at 5° for two months, resulted in appreciable mortality rates among corms. Treatments above 20° for one or two months were 100 % lethal. Removal of the discs of old corms, together with the old leaf-bases, also affects the onset of sprouting and sprouting of the group as a whole proceeded 5 to 14 days earlier than in the normal corms.

Table 7. Sprouting response of temperature treated W. humilis corms.

No. of corms	treatment	ultimate sprouting response after treatment.	
		1 month	2 months
10	0°+oc	50%	10%
10	5°+oc	90%	0%
10	5°-oc	100%	40%
10	10°+oc	100%	100%
10	10°-oc	100%	100%
10	15°+oc	70%	0%
10	15°-oc	0%	0%
groups of 10	20-35°-oc	0%	0%

None of the corms treated for one or two months flowered during the 1973/4 flowering season. Some corms however, transplanted at the same time as the 4, 8 and 16-hour wet heat treatments, came into flower. These are enumerated in Table 8.

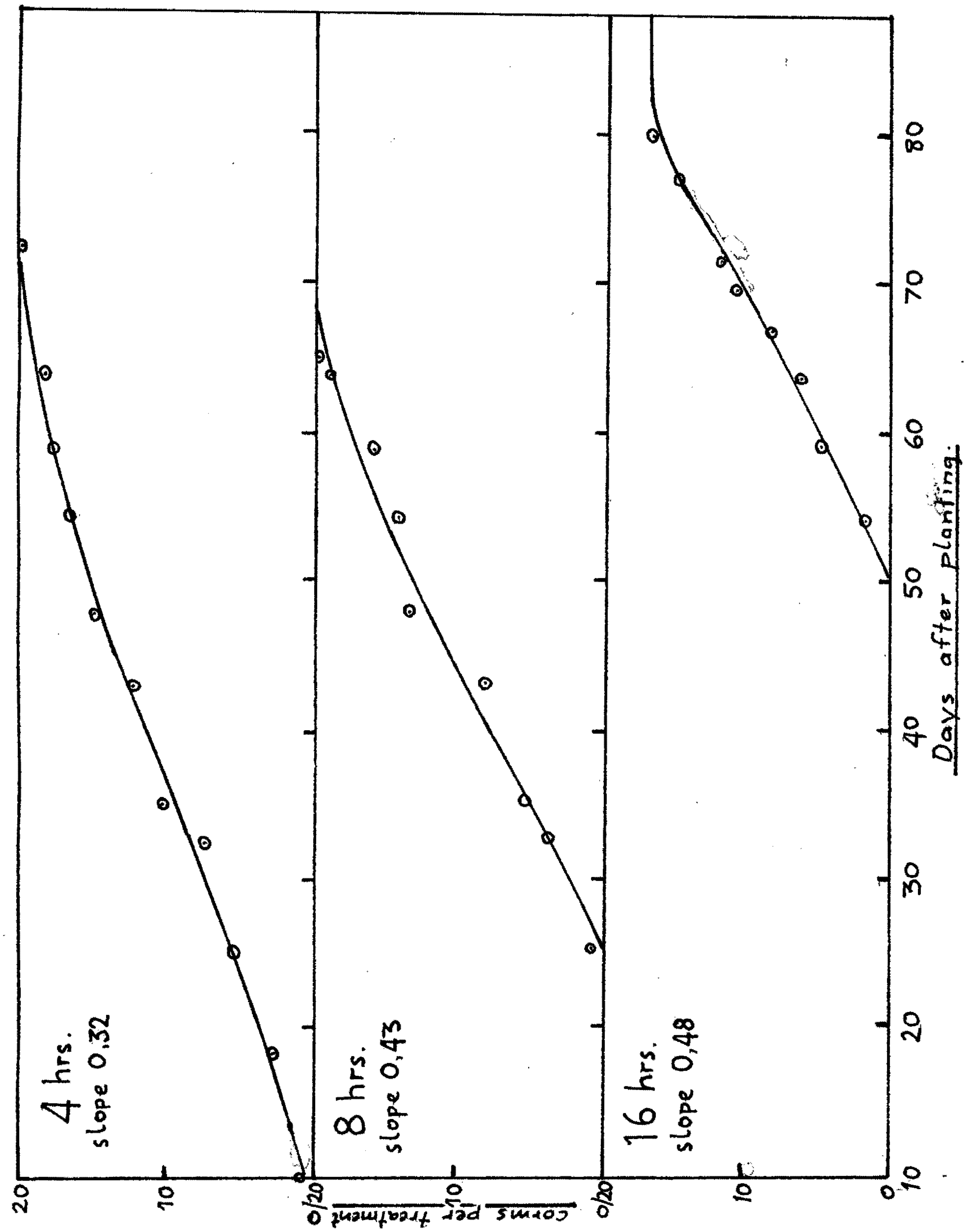


Figure 8. Sprouting response of W. humilis corms planted on 5-6-'73 after a 4, 8 and 16 hour treatment in water at 40°. First sprout up on 15-6-'73.

In transplanted corms which had flowered during the 1972/3 flowering season a marked increase in multiple sprouts was observed, compared to the control group which had not flowered in 1972/3. A control group consisting of the smallest corms failed to flower altogether. The flowering response in all groups was very poor.

Table 8. Flowering behaviour of W. humilis corms in 1973/4 transplanted shortly after lifting on 3.5.1973 into prepared open ground at the University of Cape Town nursery.

No	treatment or description	% sprouting	% flowering	% with multiple sprouts
20	smallest corms, +oc	70	0	0
"	flowered previous year +oc	100	10	90
"	non-flowering previous year, -oc	100	20	30
"	non-flowering previous year, +oc	100	10	
"	4 hrs. 40° wet treatment	100	20	
"	8 hrs. " " "	100	10	
"	16 hrs. " " "	90	0	

3. Germination experiments on Watsonia spp. seed.

Mature seed of W. tabularis and W. humilis was collected from pods in the field. Approximately 90% of the seed was damaged by beetle larvae and only visibly undamaged seed was selected for the following experiments. Groups of 10 to 20 seeds were selected at random and incubated on damp filter paper inside sterile petri dishes at various temperatures. To decrease the incidence of fungal attack it was necessary to mechanically wash the seed in a " rotating" washing unit with sterile water. Four changes of water were made during a one-hour washing period and the incidence of fungal attack was markedly reduced.

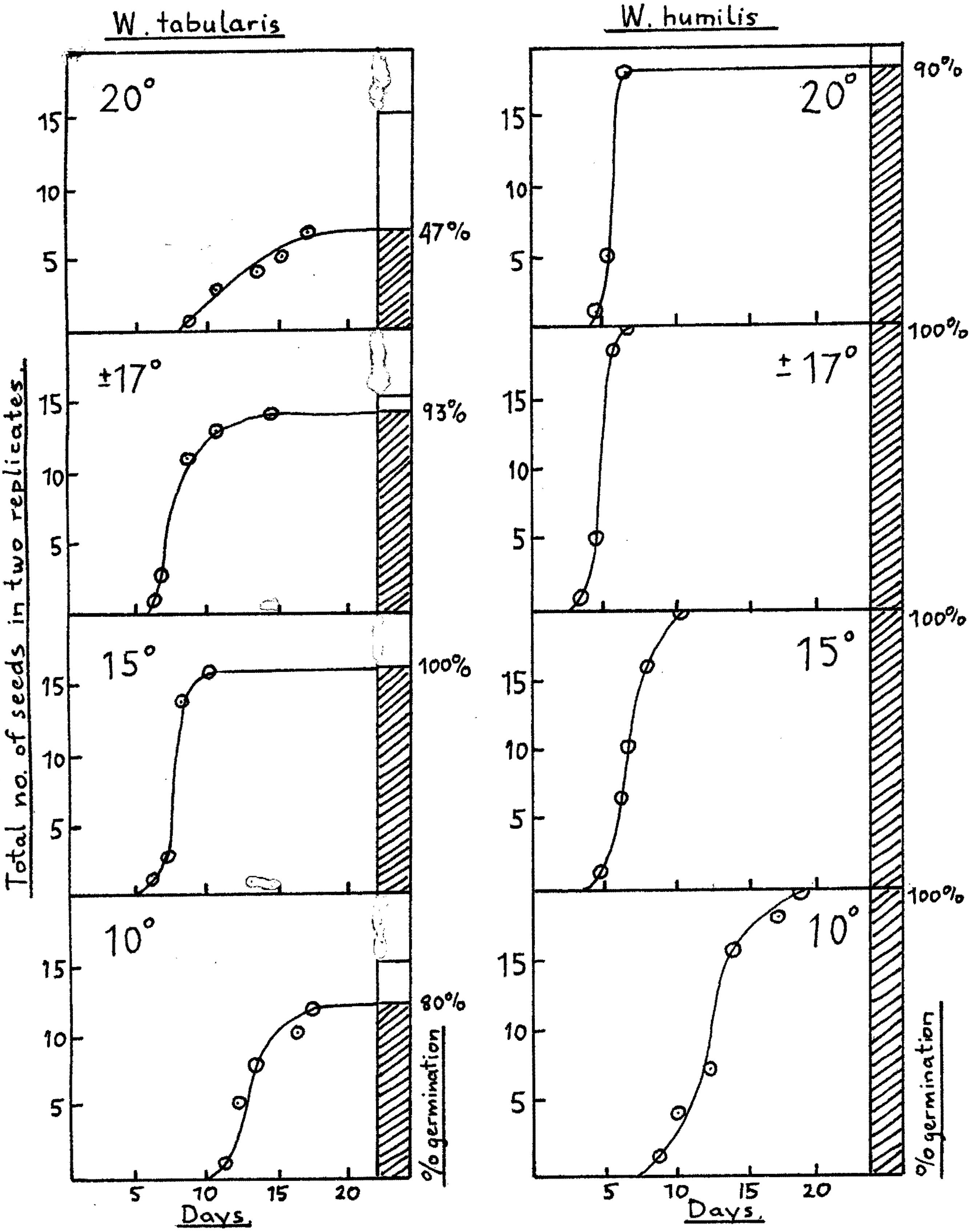


Figure 9. Germination response of Watsonia spp. seeds at various temperatures.

Note: The pre-treatments are shown in the top left corner of each graph. "Heat" is a 40°/4-hour treatment in aerated water before the start of the incubation period at the temperature indicated.

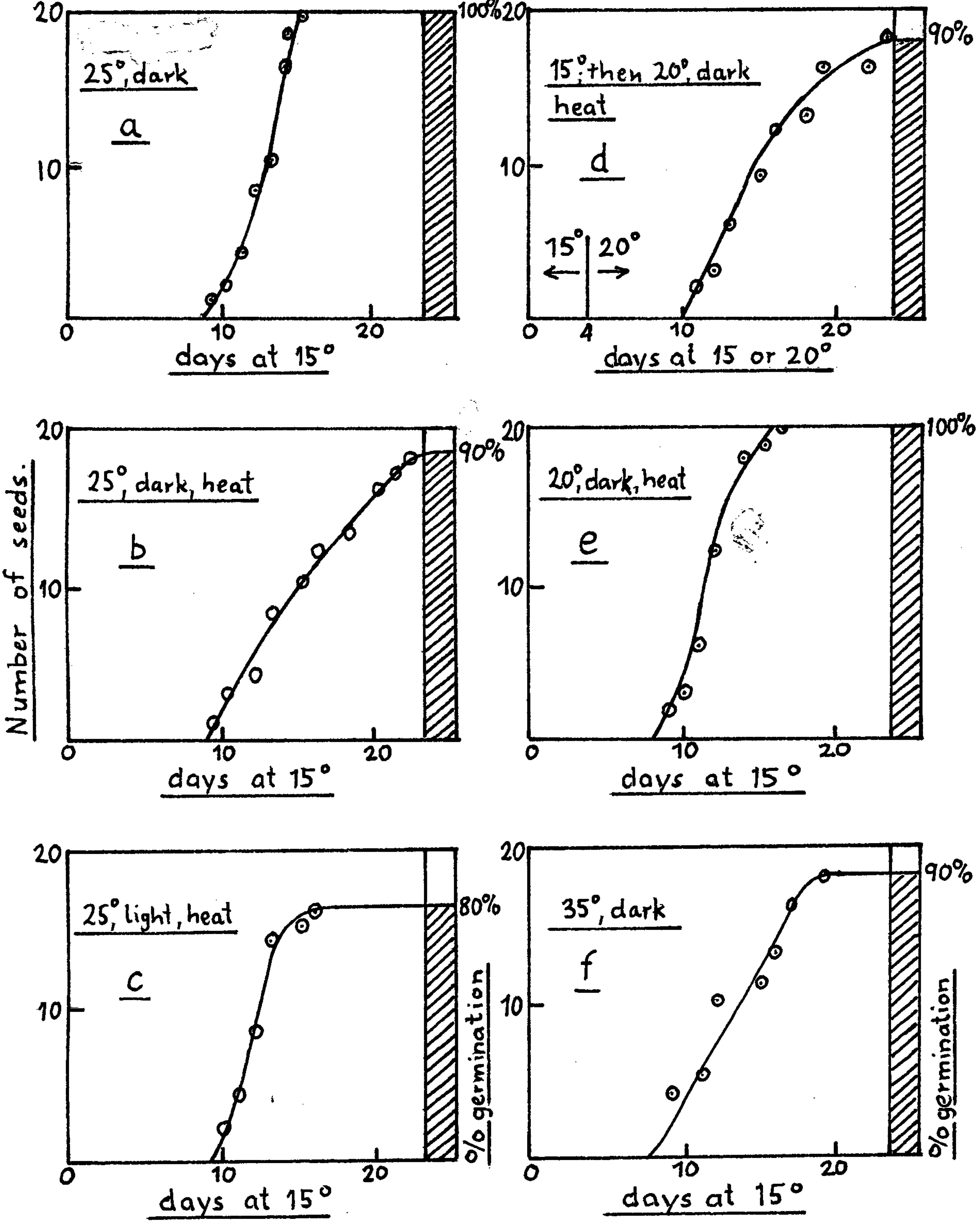


Figure 10. Germination response of W. tabularis seed after various unsuccessful pre-treatments in the dark or in light.

Most seeds were incubated in the dark but some groups received light treatment using a 150 w. tungsten filament lamp suspended 1 m. above the seeds. Sometimes a short four-hour heat-treatment of seeds in aerated distilled water was used prior to incubation.

Seeds were collected during May 1973 and experiments were conducted before September 1973. The results of the study are shown in figures 9 and 10.

In both W. tabularis and W. humilis seed no germination occurred at temperatures below 5° or above 25°C, after six weeks' incubation. Temperatures of 35° for over four weeks did not affect the viability of W. tabularis seed, as such seed, transferred to a suitable temperature regime, showed 100% germination. Optimum temperatures for seed germination in W. tabularis and W. humilis appeared to be between 15° and 18°. At temperatures above and below the optimum conditions, the lag phase, (between the start of incubation and the emergence of the radicle), increased, and the gradient of the "germination curve" decreased. Light also appeared to affect the germination curve, as graphs b and c of figure 10 show. In the sample of seeds receiving light the gradient of the germination curve was steeper in gradient than that of the sample germinated in the dark.

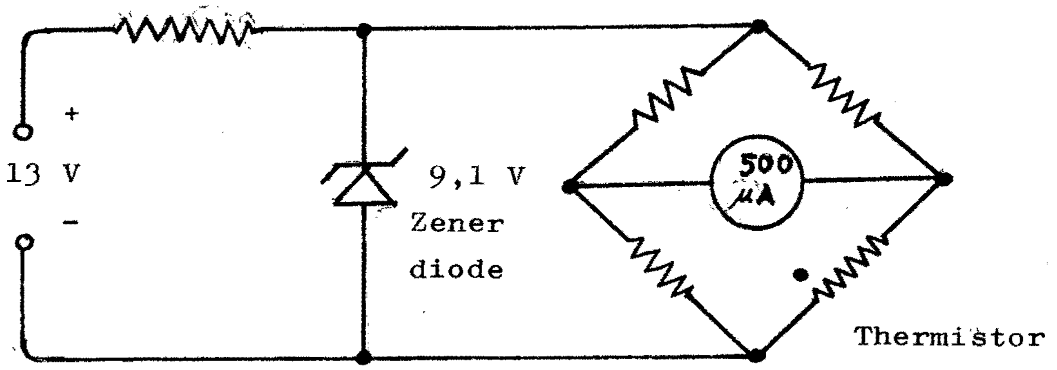
A pre-treatment of seeds at 40° before incubation decreased the slope of the germination curve, which is illustrated in figure 10. The viability of seeds was also affected, as 15% of pre-treated seeds failed to germinate after six weeks incubation at their optimum germination temperature of 15°C...(figure 10, graph b) A pre-treatment at 40° for four hours suppressed subsequent germination during incubation at 20° in both species, but the same 40°/4 hour pre-treatment of W. tabularis seed, followed by 4 days of incubation at 15° and then at 20°C, resulted in 90% germination being obtained. (Figure 10, graph d).

5. TEMPERATURE EFFECTS OF MULCHING AND BURNING.

Measurement of sub-soil veld-fire temperatures.

Sub-soil temperatures during the experimental burn on the *W. tabularis* plot were recorded by thermistors. Stantel type A 1 451 100 thermistors with a resistance of 10 k ohm at room temperature were used in the bridge circuit shown in figure 11.

Figure 11. Basic circuit for temperature measurement using thermistors.



With each thermistor a series resistor was used to allow for balancing the bridge at 25°C. This enabled six thermistors to be switched rapidly in and out of circuit without unduly changing the current flow through the meter. After ageing the thermistors through repeated heat cycling a calibration graph was then prepared. This overcame the difficulty of non-linear thermistor response at the higher temperatures. Temperature differences as low as two degrees could easily be resolved by the apparatus.

The small size of the thermistor pellets, (1mm Ø), enclosed in thin glass envelopes of 3x20mm., allowed the probes to reach ambient temperature quickly. To prevent heat conduction into the thermistor pellet via the instrument leads, these were bent downwards into the soil and insulated with glass fibre sleeving and tape. The instrument leads were buried in a deep slit in the soil. No scorching of the leads occurred during the burn.

Temperature readings were obtained over a $3m^2$ area where the fire was expected to be most severe. Some additional leaf litter was added to the fire directly above thermistors No. 1 and 2 30 minutes after the start of the fire, in order to intensify the blaze. (figure 12)

Fires in dense scrub should be capable of producing far higher temperatures however.

Temperatures under vermiculite mulches.

Vermiculite mulching materially affects sub-soil temperatures, and appears to aid in retaining soil moisture. Typical maximum temperature differences at 6 cm under bare soil and under soil mulched to a depth of 3-5cm amounted to about 4^o C in the early afternoon, during summer. The mulched soil remained decidedly cooler during summer, but in winter the opposite appeared to be the case. Mulched soil then was found to be up to 1^o degree warmer than non-mulched soil.

Typical soil temperatures during early morning at a depth of 6 cm were around 12^o during winter and 17^o during summer. Later in the day they rose to around 15^o and 28^o C respectively.

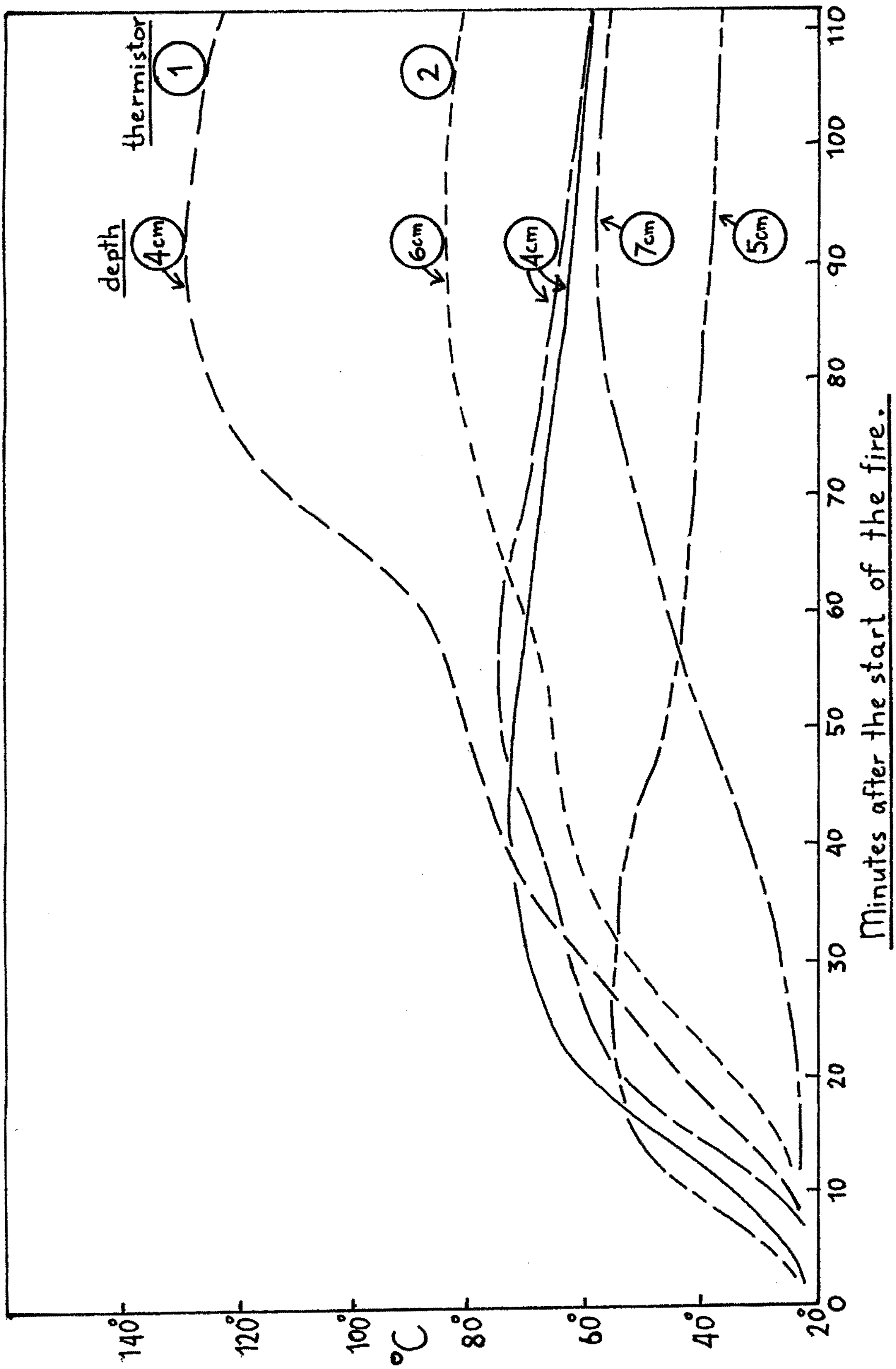


Fig. 12. Soil temperatures during an experimental veld fire.

6. CARBOHYDRATE STUDIES

1. Introduction.

Sometime during a growth cycle, the aerial parts of a geophyte die back, and the vital functions of the plant are maintained by the apparently quiescent underground organs. Finally fresh growth is initiated from these organs, resulting in a new cycle of development. Reserve food stores, maintained inside the underground organ, play an important part in this development. It is of interest how these food reserves are stored in a form which does not create osmoregulatory problems for the plant, yet can readily be made soluble and hence mobile to enable their utilization at the sites of growth. The mechanisms which trigger and control these responses in the dormant organ must also be elucidated.

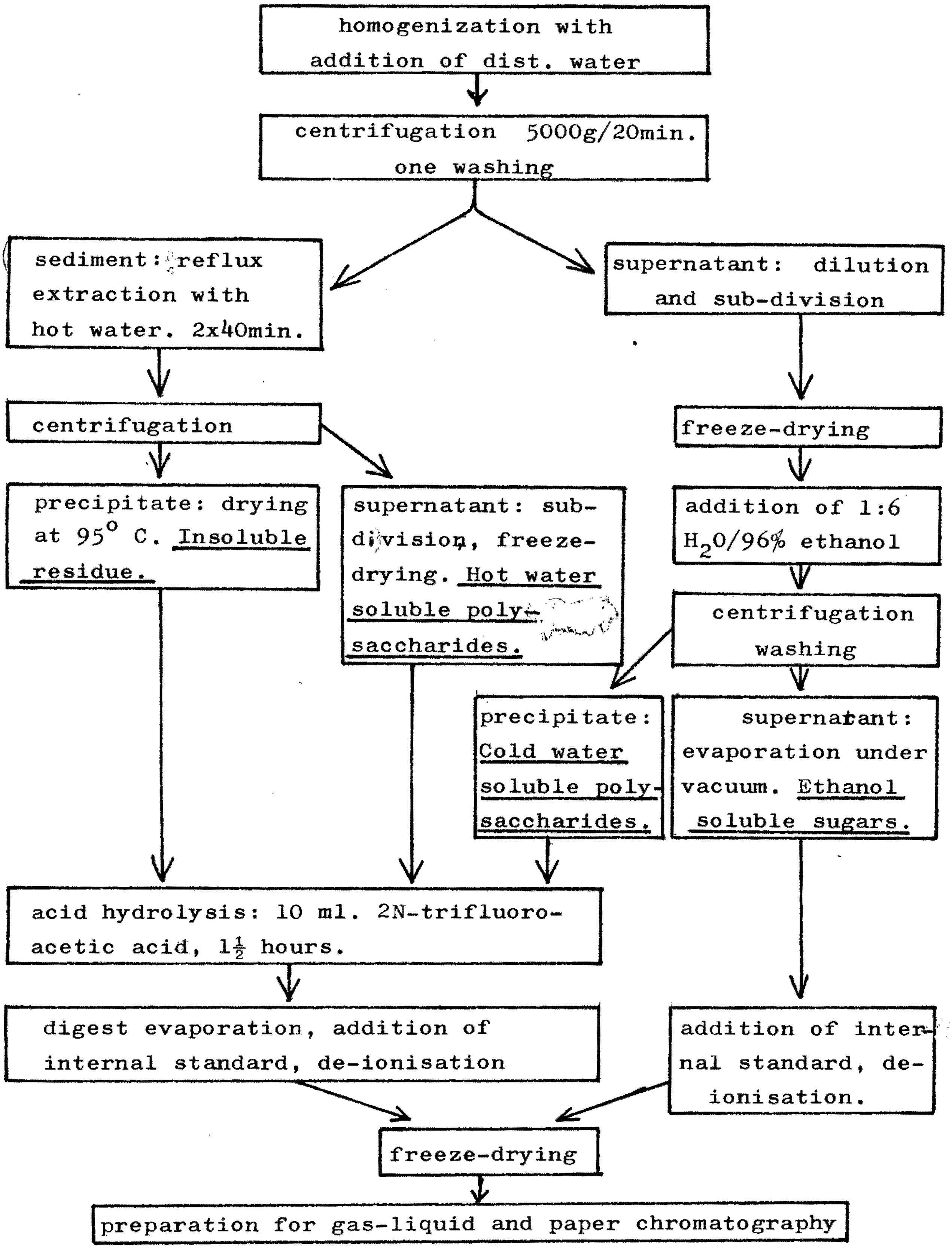
In many underground storage organs, such as potato tubers and yam roots, starches form the main food reserve. A simple iodine test shows that this is not so in watsonia corms. Instead, a gummy mucilage, exhibiting colloidal properties, is found inside large sacs traversing the corm. (W. pyramidata (Andr.) Stapf., Shaw 1965). The virtual disappearance of similar mucilage during the intense growth period of the Cape W. tabularis, W. humilis and W. pyramidata, lends weight to the presumption that these substances could be or be part of the reserve food stores of these plants. After the basic cellular structure of new developing corms has been laid down, the mucilaginous substances are slowly built up again in the mucilage-sacs.

Primary cell-walls of spermatophyte plants consist mainly of hemi-celluloses and cellulose. While cellulose can be carefully hydrolysed to cellobiose, a disaccharide composed of two glucose units, and finally to glucose only, the hemicelluloses yield mixtures of the sugars composing them, upon strong hydrolysis. In the middle lamella between cells pectic substances are found while interspersed among the microfibrils of the cell-wall small amounts of suberin, lignin and acidic substances, such as proteins, may be found. Some hemicelluloses are water soluble, while some of the storage products enclosed by the cells may be partially soluble, for instance the amylose component of starch. In the case of the mucilaginous gums found in watsonia corms-sacs viscous colloidal solutions may form. In order to analyse watsonia corms it is necessary to physically fractionate all these components, subdivide the fractions and then hydrolyse individual polysaccharides into their component sugars. Every method of fractionation offers benefits as well as disadvantages, and the method employed has tried to compromise between these.

1) Corm extraction procedure.

Immediately after collection corms were cleaned of all leaves and root material. The green leaves were cut off close to the top of the corms and all leaf bases were stripped off, so as to expose the internodes of the corms. The corms of the current and the last season were then weighed separately. Five corms were used to obtain a composite sample of material for chemical analysis. As fresh material was in limited supply it was impossible to always choose similar sized corms for each analysis, as corm size can only be judged approximately from the size and pattern of leaves produced by the plant above ground. Corms were cut with a knife and similar quantities of material from each corm were taken and combined in a sample of 5-10 g fresh weight. This sample was homogenized in a mortar and pestle, after addition of some distilled water, and treated further as outlined in the flow diagrams of figure 13.

Figure 13. Flow diagram of corm polysaccharide analysis.



3. Gas liquid chromatography of sugars.

Tri-methyl-silyl derivatives were prepared in 50 ml. pear-shaped flasks, using a method similar to that of Holligan and Drew (1971). Samples were dissolved in 0,85 ml. pyridine and 0,1 ml. hexamethyldichlorosilasane (HMDS) and 0,05 ml. trimethylchlorosilane (TMCS) were added in quick succession and agitated for 30 seconds on a Fison's Whirlimixer. A fine white precipitate forms during the reaction, but before withdrawing samples after an interval of at least 2½ hours this was resuspended by further agitation. Samples of 2-10 μl were withdrawn with a 10 μl Scientific Glass Engineering syringe fitted with an 11,5 cm long needle and injected into one of the injection ports of a Dual Column Pye Unicam Gas Chromatogragh Series 104 with an attached Philips PM 8000 pen recorder. Mono- and oligosaccharides were separated in 2,1 x 0,006 m glass columns containing a non-polar liquid phase S.E. 52 (2% methyl phenyl silicone gum) on a Diatomite CQ (80-100 BSS mesh) solid support. Flow rate of the nitrogen carrier gas was 30ml/min. and the temperature program commenced with an isothermal 140^{o} run for 4 min., followed by a 6^{o}/min. temperature increase to 290^{o} and a final isothermal run at 290^{o} for 20 minutes.

Sugars were identified by comparison of their retention times with standard sugars and variations in the detector response were compensated for by the use of erithritol as an internal standard, which was present in every sample injected. Quantitative determinations were made by measuring sugar peak heights on the recorded traces and referring to calibration curves prepared for each sugar component. Partially resolved sugar peaks (β- mannose, β- galactose and α- glucose) were resolved by reference to their free anomer peaks. Mol-% of sugar was calculated using K-values referred to erythritol, used as the internal standard. K-values were calculated using the following formula:

$$K = \frac{\text{peak height of sugar}}{\text{weight}} \div \frac{\text{peak height of erythritol}}{\text{weight}}$$

The values obtained for K were then inserted in an equation to obtain the molar proportions of the sugars present in the sample:

$$\text{molar proportion} = \frac{\text{peak height of sugar}}{\text{K x mol.wt. of sugar}}$$

The mol-% of each sugar could then be calculated from the following equation:

$$\text{mol-\%} = \frac{\text{molar proportion of sugar}}{\Sigma(\text{molar proportions of sugars})} \times 100$$

Co-chromatography with known sugars was sometimes employed to confirm the identity of sugars present in the reaction mixture. Sufficient chromatograph response could often be obtained by adding the known sugar to the prepared reaction mixture and introducing further aliquots of sililating reagents.

4. Paper chromatography of sugars.

Sugars were also confirmed by running one-dimensional descending chromatograms in a ethyl acetate / acetic acid / water mixture in a 14 : 3 : 3 ratio.

Table 9 Sugars identified by paper chromatography.

sugar	gluc.	sucr.	fruct.	xyl.	mann.	arab.	gal.
Ethanol soluble fraction	+	+	+	+	?	-	-
Hot water hydrolysate	+	-	-	+	+	+	+
Cold water hydrolysate	+	-	-	+	+	+	+

Key:

gluc. = glucose
sucr. = sucrose
fruct. = fructose
xyl. = xylose
mann. = mannose
gal. = galactose
arab. = arabinose

Silver nitrate (Hough et al 1950) and p-anisidine hydrochloride (Trevelyan et al 1950) were used as detection reagents.

Sugars were identified by running mixtures of expected sugars (from G.L.C. results) concurrently with unknowns. Identifications were then confirmed by comparison of the colour reactions and retention times of the known sugars.

5. Carbohydrate composition of W. humilis corms.

To obtain results on the distribution of carbohydrate levels in individual corms, four mature and currently leafing W. humilis corms were analysed on 15-8-73. The second-youngest corms (=old corms) of two plants were also analysed, but no developing new corms were seen. The data is presented in the following tables.

Table 10. Moisture content and fresh weight of W. humilis corms.

Corm	A	B	C	D
weight new corm, g	7,30	10,28	10,75	7,36
" old corm, g	1,76	2,80		
moisture new corm	74,1%	73,5%	69,9%	78,6%
" old corm	75,9%	75,1%		

Table 11. Ethanol soluble sugars, mg/g dry weight. W. humilis.

corm	sucrose	glucose	inositol	fructose*
new corm A	11,9	2,0	0,2	0,8
" " B	15,2	2,7	0,9	1,8
" " C	12,5	3,9	0,8	3,0
" " D	41,4	8,9	2,1	5,5
mean	20,3	4,4	1,0	2,8
old corm A	30,2	9,2	1,0	3,3
" " B	73,0	10,7	1,5	5,5
mean	51,6	10,0	1,3	4,4

* Note: Small amounts of mannose were detected by paper chromatography, but the bulk of the sugar appears to be fructose.

Table 12. Cold water soluble polysaccharide in corms of W. humilis in mol-% and mg/g dry weights.

Mol-%

corm	arab.	xyl.	mann.	gal.	gluc.
new corm A	39,3	16,0	6,6	22,3	15,7
" " B	37,5	16,0	5,3	27,1	14,1
" " C	37,7	17,6	4,1	30,4	10,2
" " D	39,0	16,5	5,0	26,7	10,9
mean	38,4	16,6	5,2	26,6	12,7
old corm A	45,4	20,9	2,6	6,9	24,3
" " B	40,2	17,2	3,2	26,9	12,5
mean	42,8	19,0	2,9	16,9	18,4

continued

Table 12. cont.

Concentration mg/g dry weight

corm	arab.	xyl.	mann.	gal.	gluc.
new corm A	6,0	2,3	1,2	4,2	3,1
" " B	6,4	2,6	1,1	5,6	2,9
" " C	7,7	3,4	1,0	7,5	2,6
" " D	6,0	2,4	0,9	5,4	2,1
mean	6,5	2,7	1,1	5,7	2,7
old corm A	6,1	2,7	0,4	1,0	3,9
" " B	6,9	2,8	0,7	5,6	2,6
mean	6,5	2,8	0,6	3,3	3,3

Table 13. Hot-water soluble polysaccharide, W. humilis in mol-% and mg/g dry weight.

Mol-%

corm	arab.	xyl.	mann.	gal.	gluc.
new corm A	26,9	12,1	1,8	14,4	44,8
" " B	5,6	3,5	2,9	55,6	32,4
" " C	5,5	4,0	14,8	55,7	19,9
" " D	14,8	7,6	1,9	13,0	63,3
mean	13,0	6,8	5,4	34,7	40,1
old corm A	2,7	1,9	10,0	42,9	42,5
" " B	6,7	4,8	2,0	6,0	80,5
mean	4,7	3,3	6,0	24,5	61,5

continued

Table 13 cont.

Concentration mg/g dry weight.

corm	arab.	xyl.	mann.	gal.	gluc.
new corm A	14,6	6,1	1,1	9,1	28,5
" " B	5,5	3,5	2,2	69,4	40,7
" " C	6,0	4,2	19,5	73,2	26,4
" " D	11,0	5,6	1,8	12,2	59,9
mean	9,3	4,9	6,2	41,0	38,9
old corm A	1,6	2,4	17,0	73,2	72,8
" " B	6,0	4,1	2,0	7,2	87,8
mean	3,8	3,3	9,5	40,2	80,3

The total amounts of sugars detected in the ethanol soluble, cold and hot water soluble polysaccharide fractions are shown in table 14. The hot water insoluble fraction, ("insoluble residue" in figure 13) has not been included in the table as this fraction appears to consist mainly of the hydrolysis products of cell-wall material, and is quite similar in corms A - D.

Results indicate that the sugar components of the cold water soluble polysaccharide fraction occur in similar ratios in all four current or new corms, regardless of corm size. In the old corms of plants (A and B) there is, however, an appreciable difference in galactose levels. In the ethanol and hot water soluble fractions appreciable differences in the sugar composition of the fractions occur between corms. There possibly is a relationship between corm size and level of arabinose and galactose in the hot water soluble fraction, as the two lighter corms (B and C) have arabinose levels only $\frac{1}{3}$ of those found in the heavier corms, (A and D). In the heavier corms again there appears to be a greater proportion of galactose, compared with the light corms.

Table 14. Mg/g weight of sugar and polysaccharide components in the ethanol, cold and hot water soluble fractions of W. humilis corms.

corms	fraction soluble in : ethanol	cold water	hot water	mg/g dry wt.	mg per corm.
new A	14,9	16,8	59,4	91,1	172,2
" B	20,6	18,6	121,3	160,5	437,2
" C	20,2	22,2	129,3	171,7	555,6
" D	57,9	16,8	90,5	165,2	260,2
old A	43,7	14,1	167,0	224,8	94,4
" B	90,7	18,6	107,1	197,8	138,5

As the composition of the cold water soluble fraction shows only small fluctuations, a five-corm sample is adequate to assess cold water soluble polysaccharide levels in a small population of plants. For the hot water and ethanol soluble fraction this is not the case, as a five-corm sample will only give a rough assessment of the expected sugar-levels.

Totalling the amounts of sugar in the three fractions for each corm; (Table 14) it is seen that there is a relatively greater concentration of sugar in the heavier corms, as opposed to the lighter ones. For the heavier corms (B and C) the ratio of corm dry weight to weight of sugars detected in the three fractions is 6:1, and for the light corms 8:1.

6. The relationship between corm age and carbohydrate composition.

Two W. humilis plants were collected from the field on 15-3-73 and from each plant the currently leafing corm as well as three progressively older corms, (labelled '72-'70 ? in table 15) were analysed for carbohydrate levels. The presence of single and distinct "old corms"suggested that neither plant had flowered during the previous three years, as flowering in W. humilis usually results in several corms being produced during the following season. At the time when they were collected the currently leafing "new corms" had not yet reached maturity, as the fresh weight ratio of the new corms to the second-oldest corms was only 2:1, whereas in mature "new corms" the ratio is often greater than 3:1. From table 15 it can be seen that the fresh weight of "old corms" remains relatively constant but that the water content of these corms increases annually.

Table 15. Weight and moisture content of a W. humilis corm age-series.

Season		'73	'72 ?	'71 ?	'70 ?
fresh corm weight/g plant	A	5,5	2,9	2,6	2,9
" " " "	B	4,9	2,1	2,7	1,8
% moisture "	A	59,0	60,6	61,5	66,8
" " "	B	56,7	60,4	62,2	66,7

The relative proportions of sugars after hydrolysis in the hot and cold water soluble fractions are given in table 16, while the ethanol soluble carbohydrates are shown in table 17.

In the ethanol soluble carbohydrates, shown in table 17, the cyclic polyol inositol was identified by co-chromatography. Two unidentified compounds with retention times of 1,02 and 1,03 relative to sucrose were found. Paper chromatography indicated that mannose may be present in the samples, however the amounts of mannose present appear insignificant in proportion to the other sugars detected. On traces obtained from the gas-liquid chromatography analysis, the mannose peaks unfortunately coincide with fructose.

Table 16. Mol-% of hot and cold water soluble sugars in W. humilis corms of different ages.

Cold water soluble sugar fraction.

Plant A	arab.	xyl.	mann.	gal.	gluc.	rhamn.
'73	17,9	7,3	3,5	19,1	46,1	6,2
'72 ?	40,4	19,9	3,2	23,4	9,2	4,0
'71 ?	46,4	15,8	3,2	20,1	10,1	4,3
'70 ?	34,6	14,9	2,6	24,4	16,9	6,5
Plant B						
'73	21,6	14,2	4,7	23,7	24,7	11,0
'72 ?	35,8	20,4	3,1	24,6	10,8	5,3
'71 ?	38,7	19,6	3,2	25,2	8,3	5,0
'70 ?	22,5	12,3	2,1	16,2	24,3	4,6

Hot water soluble sugar fraction.

Plant A	arab.	xyl.	mann.	gal.	gluc.	rhamn.
'73	1,6	1,4	17,8	72,4	6,8	t
'72 ?	2,8	t	9,9	56,0	31,4	t
'71 ?	6,1	3,8	2,3	3,7	84,1	t
'70 ?	4,0	2,3	5,0	26,6	62,1	t
Plant B						
'73	0,2	2,8	12,4	61,0	23,5	t
'72 ?	4,4	2,1	1,3	4,0	88,2	t
'71 ?	2,8	1,9	15,5	67,9	12,0	t
'70 ?	9,0	4,6	t	t	86,4	t

t = trace, just discernible on G.L.C. chart at 32 x 10^3 attenuation.

Table 17. Ethanol soluble sugars in W. humilis corms of different ages. Mg/g dry weight.

Plant A	fructose	glucose	inositol	sucrose
'73	2,4	9,1	1,3	16,5
'72 ?	1,1	6,4	0,4	19,8
'71 ?	1,3	4,3	t	16,2
'70 ?	t	t	t	4,2
Plant B				
'73	2,8	14,3	1,2	18,6
'72 ?	3,1	8,0	0,4	17,5
'71 ?	2,1	2,7	t	2,0
'70 ?	t	t	-	10,7

Acid hydrolysis of the insoluble fraction, obtained after separation of the hot water soluble fraction, yielded mainly glucose. Arabinose, xylose, mannose and galactose levels were very small. This appears to indicate that the bulk of the insoluble fraction is derived from cellulose cell wall material. The small amounts of cellobiose and oligosaccharides detected are probably due to incomplete hydrolysis of this fraction.

The dry weights of the insoluble residues, obtained after removal of the ethanol, cold and hot water soluble components, are shown in table 18.

Table 18. Mg/g dry weights of insoluble components obtained from W. humilis corms.

Season	'73	'72 ?	'71 ?	'70 ?
Plant A	0,155	0,181	0,220	0,155
Plant B	0,203	0,189	0,163	0,170

7. Carbohydrate composition of W. humilis and W. tabularis leaves.

Leaves of W. humilis from the field were analysed during spring 1973. The ethanol, cold and hot water soluble fractions were investigated and a comparative study was made using W. tabularis leaves. A comparative account of the results is given below.

Table 19. Leaf ethanol soluble sugars, mg/g dry weight 19-11-73.

Sugar	gluc.	fruct.	sucr.	inos.	% moisture
W. tabularis	6,34	1,71	0,39	0,30	73%
W. humilis	10,95	3,35	2,55	1,50	70%

inos. = inositol

Table 20. Leaf cold water soluble polysaccharide components, mg/g dry weight. 19-11-73.

Sugar	arab.	xyl.	mann.	gal.	gluc.	unid*	total
W. tabularis	3,61	1,71	0,26	1,73	0,45	0,10	7,86
W. humilis	1,57	1,63	1,08	1,40	1,77	4,14	11,59

*Note: A peak with a retention time of 1,086 - 1,089 relative to β- glucose was found. At this position inositol, if present in the sample, would be expected. The weights of the unidentified sugar were therefore calculated by assuming the unknown component to have a detection response similar to that of inositol.

Table 21. Leaf hot water soluble sugar components, mg/g dry weight. 19-11-73.

Sugar	arab.	xyl.	mann.	gal.	gluc.	unid.	total
W. tabularis	0,71	0,38	0,16	0,50	0,56	0,05	2,36
W. humilis	1,38	0,68	0,60	1,90	2,14	0,35	7,05

Table 22. Mol-% of leaf cold and hot water soluble sugars.

Cold water soluble, mol-% 19-11-73.

Sugar	arab.	xyl.	mann.	gal.	gluc.	unid.
W. tabularis	48,2	24,1	2,9	19,1	4,9	0,9
W. humilis	13,6	14,9	7,7	17,6	29,5	16,8

Hot water soluble, mol-% 19-11-73.

Sugar	arab.	xyl.	mann.	gal.	gluc.	unid.
W. tabularis	33,0	18,4	6,0	19,3	21,6	1,7
W. humilis	22,6	11,5	8,0	25,6	28,6	3,8

Leaves of W. humilis were analysed at an interval of two months, a comparison of the analyses being given below.

Table 23. Ethanol soluble leaf sugar of W. humilis, mg/g dry weight, on two dates.

Date	glucose	fructose	sucrose	unid.*	total
19-11-73	10,95	3,35	2,55	1,50	18,35
19-9-73	6,43	2,20	1,13	1,49	11,25

*See note below table 20.

Table 24. Mol-% of cold and hot water soluble polysaccharide components of W. humilis leaves on two dates.

Cold water soluble

Date	arab.	xyl.	mann.	gal.	gluc.	unid.
19-11-73	13,6	14,9	7,7	17,6	29,5	16,8
19- 9-73	15,8	17,2	14,6	15,4	24,7	12,2

Hot water soluble

Date	arab.	xyl.	mann.	gal.	gluc.	unid.
19-11-73	22,6	11,5	8,0	25,6	28,6	3,8
19- 9-73	20,0	8,5	6,0	32,1	29,3	4,1

The combined weight of the ethanol, cold and hot water soluble sugars was 36,99 mg/g on 19-11-73 and 28,34 mg/g on 19-9-73. This represents a dry weight increase of 8,65 mg/g over the two-month period. From table 23 it is evident however that this increase in dry weight is almost entirely due to a heavier ethanol soluble sugar fraction on the 19-11-73.

8. Seasonal carbohydrate levels in W. humilis corms.

Studies were performed on fluctuations in the carbohydrate content of non-flowering W. humilis plants growing in the field during 1972-'73. Samples usually consisted of five corms and the tri-methyl silyl derivatives of each fraction were again analysed.

Table 25. Cold water soluble sugar components in "new" and "old" corms of non-flowering W. humilis plants, mg/g dry weight.

New corms

Date	arab.	xyl.	mann.	gal.	gluc.	rham.	total
19- 9-72	t	t	1,52	-	4,32	t	5,84
10-12-72	2,64	1,08	-	1,72	1,12	t	6,38
20- 1-73	4,64	2,97	t	3,37	1,72	t	12,70
18- 2-73	4,09	2,32	t	3,50	1,62	-	11,53
15- 3-73	2,57	1,26	0,65	3,36	6,08	1,18	15,10
12- 4-73	3,62	3,10	1,25	3,62	2,85	t	14,44
13- 7-73	13,35	4,20	1,00	5,10	1,20	t	24,85
15- 8-73	6,50	2,70	1,10	5,70	2,70	-	18,70

t= trace
-= absent

= two plants
= four plants

Old corms

Date	arab.	xyl.	mann.	gal.	gluc.	rham.	total
19- 9-72	0,9	0,6	0,9	1,1	1,6	1,9	7,0
10-12-72	5,3	2,6	t	3,9	0,6	t	12,4
20- 1-73	5,3	2,4	t	3,2	1,1	-	12,0
18- 2-73	4,0	3,2	t	3,9	2,2	-	13,3
15- 3-73	6,9	3,5	0,7	2,8	2,2	0,9	17,0
12- 4-73	3,4	2,7	1,5	3,2	2,1	t	12,9
13- 7-73	9,4	5,2	0,7	5,3	0,9	-	21,5
15- 8-73	5,2	2,3	0,9	4,6	2,7	t	15,7

From table 25 it appears that the levels of cold water soluble sugar components are fairly similar in both the corms of the current season, (new corms) as well as in the "old" corms of the previous season. The hot water soluble sugar components increase from 15,3 mg/g dry weight when the corms are immature to over 100 mg/g when the corms have reached maturity (table 26).

At this final mature state the development of a new corm is imminent. In "old corms" there is also an increase in the hot water soluble sugar components, the increase is however not as marked as in the "new corms".

Both these increases, in the new as well as in the old corms, appear to be primarily due to increasing concentrations of galactose. In "new corms" there is also a significant rise in the glucose level during the development and maturation of the corm, but this glucose increase is not found in the "old corms".

Table 26. Hot water soluble sugar components in "new" and "old" corms of non-flowering W. humilis plants, mg/g dry weight.

New corms

Date	arab.	xyl.	mann.	gal.	gluc.	total
19-9-72	4,4	1,5	t	4,5	4,9	15,3
21-1-73	2,6	1,2	1,8	4,0	8,4	18,0
15-3-73	1,1	1,2	14,0	61,8	17,0	95,1
13-7-73	6,3	2,0	12,0	36,1	25,2	81,6
15-8-73	9,3	4,9	6,2	41,0	38,9	100,3

Old corms

Date	arab.	xyl.	mann.	gal.	gluc.	total
19-9-72	6,6	3,6	2,3	6,9	49,3	68,7
21-1-73	2,6	1,4	0,8	2,4	27,2	34,4
15-3-73	2,5	0,6	6,4	35,1	46,6	91,2
13-7-73	3,4	3,2	4,2	64,0	40,2	115,0
15-8-73	3,8	3,3	9,5	40,2	80,0	136,0

Table 27. Ethanol soluble sugars in new corms of non-flowering *W. humilis*, mg/g dry weight.

Date	fructose	glucose	sucrose	inositol	total
19-9-72	t	2,7	5,1	t	7,8
20-1-73	2,3	10,6	16,5	0,8	30,2
15-3-73	3,2	14,3	17,3	1,6	36,4
12-4-73	2,0	18,2	8,4	1,3	29,9
13-7-73	1,1	12,3	17,9	0,8	32,1
15-8-73	2,8	4,4	20,3	1,0	28,5

The ethanol soluble sugars found in new corms of non-flowering *W. humilis* are shown in table 27. The values of the sugars appear to be relatively uniform throughout the year, except for the low values found when the corm is in an early stage of development. On the 12-4-73 a sudden rise in the glucose level and sharp drop in sucrose level occurred. This co-incides with the development of new shoots in the corms, which had been quiescent until then. Very wet weather since the 15-3-73 had caused the ground to become soaked after a long dry summer. Before the rains the corms appeared to be inactive, with only dead leaf litter visible above ground, but by the 12-4-73 most corms had sprouted shoots of at least several cm in length.

9. Differences in the cold water soluble sugar components between flowering and non-flowering *W. humilis* plants.

Flowering of *W. humilis* plants in the field occurred from late November 1972 until well into January 1973. Whereas "new corm" development of non-flowering plants began in October, flowering plants only developed new corms with the onset of flowering in November. In flowering plants usually several new corms developed per plant, but in non-flowering plants only one corm would generally replace the previous corm. The new corms of flowering plants would rapidly increase in weight, so that by the middle of February the combined weight of the new corms produced by a flowering plant usually surpass the weight of the old one. This increase in weight appears to be more rapid than that found in new corms of non-flowering plants. (cf. figure 2 and 3)

Table 28 shows the levels of cold water soluble sugar components found in new and old corms of flowering W. humilis plants, and should be compared in conjunction with table 25.

Table 28. Cold water soluble sugar components in new and old corms of flowering W. humilis plants.

New corms

Mg/g D.W.	arab.	xyl.	mann.	gal.	gluc.	rhamn.	total
10-12-72	0,65	0,27	-	0,43	0,26	t	1,61
20- 1-73	3,27	1,78	t	2,27	1,08	t	8,40
18- 2-73	3,38	1,43	t	1,78	0,55	-	7,14
12- 4-73	1,18	0,74	0,48	1,18	0,61	-	3,01

Old corms

Mg/g D.W.	arab.	xyl.	mann.	gal.	gluc.	rhamn.	total
10-12-72	1,66	0,80	-	1,14	0,21	t	3,81
20- 1-73	2,18	0,92	-	1,34	0,61	-	5,05
18- 2-73	1,68	1,05	t	1,34	0,78	-	4,85

Whereas in non-flowering new corms a marked and regular increase in the levels of cold water soluble sugar components was found, this increase is not apparent in the new corms of flowering plants. Instead a high level of cold water soluble polysaccharide is found during late January, progressively dropping off during February, March and April. This drop appears to be correlated with seed formation in the plants.

Apart from this drop of cold-water soluble sugar levels the proportions of the components to one another are similar in both flowering and non-flowering corms, as is seen from table 29.

Table 29. Mol-% cold water soluble sugar components of flowering and non-flowering W. humilis corms on20-1-73.

W. humilis	arab.	xyl.	mann.	gal.	gluc.
flowering	41,3	23,7	t	23,7	11,2
non-flowering	37,8	26,1	2,0	22,3	11,8

10. Comparison of cold water soluble polysaccharide from W. tabularis and W. humilis.

Cold water soluble sugar components of W. tabularis and W. humilis were studied to determine interspecific differences in cold water soluble polysaccharides. A preliminary experiment had shown that ethanol and hot water soluble fractions showed great variations, therefore these fractions were no longer investigated. Corm samples were taken from five plants and collected at intervals of one to several months. The data obtained is shown in table 30.

Table 30. Mol-% of cold water soluble sugar components in non-flowering new corms of W. tabularis and W. humilis.

W. tabularis

Date	arab.	xyl.	mann.	gal.	gluc.
10-12-72	57,6	18,0	2,5	19,3	2,7
18- 3-73	41,3	27,8	4,2	17,4	9,4
6- 6-73	49,7	25,4	1,8	13,2	9,9
19- 9-73	46,9	18,2	4,2	18,0	12,8

W. humilis

Date	arab.	xyl.	mann.	gal.	gluc.
10-12-72	41,9	18,7	2,7	22,7	14,0
15- 3-73	21,7	11,8	4,5	23,5	38,5
13- 7-73	56,0	18,6	3,5	17,6	4,2
15- 8-73	38,4	16,6	5,2	26,6	12,7

Appreciable differences in the cold water soluble polysaccharide composition between the two Watsonia spp. exist.

In W. tabularis the cold water soluble sugar levels appear to remain fairly constant throughout the year, but in W. humilis large differences in the glucose and arabinose levels were detected at certain times in the year.

7. DISCUSSION

The widely held belief that spike formation in Watsonia spp. can be fire-induced has been the subject of considerable speculation. However, there may be many factors which are operating in order to stimulate flowering. In this investigation , the burning of a natural stand of W. tabularis, laboratory heat treatments, clearing of vegetation around the corms and the scattering of wood-ash over cleared plots did not result in increased flowering. Heavily mulched plots showed a reduction in flowering. During the second year after these treatments were administered, up to three times as many spikes were produced by the mulched plants compared with those of the other experimental plots. (Table 3 p. 22). The differences in the flowering response may be attributed to variations in the overall climatic conditions during 1972 and 1973; the most important of these probably being rainfall.

Evidence that water may play an important part in the flowering response of W. tabularis, may be gained from the results of the plot experiments at the University of Cape Town nursery garden during 1972-1973. The corms were planted during 1972 and were frequently watered during 1973. 60% of the largest and 27% of the smallest corms flowered during the 1973/4 season, whereas only 20% of plants growing in their natural habitat flowered. These results also suggest that the larger corms produce more flowers than the smaller ones. Other evidence that watering may be important has been observed at the Cape Point Nature Reserve. About 8000 large-cormed W. tabularis plants were planted on an earth retaining wall of a reservoir during September 1971. The plants were well-watered and the majority of them produced spikes during the following season.

Recent observations (late October, 1974) of the flowering response by W. humilis, which had been transplanted into plots at the U.C.T. nursery garden 16 months ago, have shown that 80% of the original corms have produced 2-9 spikes. No sign of spike formation was evident in the natural population at Ryan's farm. Also, plants in the field had never shown such a prolific production of leaves and flowers as had occurred amongst the transplanted population at the U.C.T. nursery gardens. The transplanted corms had always been well watered, and it is very unlikely that the natural population suffered any water shortage during the 1974 growing seasons as the 1974 winter had been exceptionally wet.

Despite the frequent watering during 1973, a very poor flowering response was obtained from W. tabularis corms transplanted into troughs at the U.C.T. nursery gardens. Yet, corms transplanted into open ground at the same site and receiving identical water regimes, showed a far better flowering response. (60 and 27%, see above).

The suggestion now arises of the involvement of growth factors, which could be leached out of the soil either by heavy watering or by rainfall. A closer examination of Bean's thesis, (1962, reported fully on p. 5 of the Introduction) has indicated that heat treated Watsonia hybrids produced more spikes when transplanted into burnt soil as opposed to unburnt ground. This result suggests that if growth factors are present they could be soil-borne and thermolabile.

Further investigations are needed to substantiate this hypothesis but these factors may play an important part in controlling the metabolism of storage reserves in the corms. Watsonia corms contain considerable reserves of carbohydrates in the form of mucilaginous gums and the chemical structure of these polysaccharides has already been investigated (Shaw, 1965). The analysis of corm storage products in this study has shown that the larger corms have a greater concentration of reserves compared with the smaller ones. Carbohydrates were divided into four fractions depending upon their solubility in ethanol and cold and hot distilled water. The proportions of the components of the cold water soluble polysaccharides remained uniform throughout a single seasonal cycle, whereas there was a considerable variation in the ethanol and hot water fractions. The hot water soluble fraction of new corms increased during their development and this increase appeared to be primarily in the form of galactose. Corms of flowering specimens of W. humilis were also studied and a reduction in the cold water soluble polysaccharides occurred at the time of seed pod development. In the non-flowering corms, there were no changes in the levels of the cold water soluble polysaccharides.

Viability of seed and seed germination have been one of the many aspects of the biology of Watsonia spp. which have been completely overlooked. Propagation of the seed is not only important in disseminating the species, but seeds as well as corms may determine the size of the future population. The optimum temperatures for germination are 15-18° but viability is not affected by temperatures up to 35°C.

In nature, the seeds fall from the pods during late summer and become wholly or partially buried at the soil surface. The high temperatures and dry conditions during summer will prevent their germination, but do not affect their viability. It is only when suitable conditions prevail, such as cooler temperatures and rains during winter, that the seeds successfully germinate.

This study has shown that simple heat treatments of W. tabularis and W. humilis corms do not directly trigger flowering. Careful observations of burnt-over corms have shown that the apical bud may be damaged by the heat of the fire and that this stimulates the development of axillary buds. This may explain why some of the "burnt" corms produce several shoots per corm; these in turn developing into new corms. Although evidence presented here is in many ways preliminary, flower initiation may depend upon a number of factors such as frequent watering, the absence of other vegetation and the presence of inhibiting "growth factors" in the soil. An answer to whether plant-soil interactions are responsible may be found by transplanting corms to fresh sterile soil every season. Annual transplantation may be sufficient to cause normal flower initiation. This, however, would be a long term project entailing several years of study. Watsonia spp. and other geophytes are an important feature of the fynbos vegetation and further investigations of their biology will be extremely useful in understanding how these plants withstand the rigours of the Cape climate.

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