THE AUTECOLOGY OF STIPA TRICHOTOMA NEES (NASSELLA TUSSOCK) ON RHODES ESTATE, IN THE SOUTH-WESTERN CAPE

A Thesis presented for the degree of

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by

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ABSTRACT

The autecology of *Stipa trichotoma* Nees (nassella tussock) was studied in the Mediterranean-type climate of the south-western Cape. The study site was Rhodes Estate, on the lower slopes of Devil's Peak. The relative growth rate of tussocks in the field was studied using non-destructive methods while more accurate biomass experiments were undertaken on nursery grown plants. These experiments revealed that nassella tussock has a relatively low growth rate with maximum growth occurring in spring to early summer. The phenology was studied for two seasons. The times and duration of flowering were noted as well as the numbers of inflorescences and fruits produced. The stages of flowering were also noted. Floral initiation occurred in early summer with fruits being dispersed in January to February. Variation in fruit shape and colour was found. Cleistogamy was found to be common and to result in relatively short fat fruits. Cleistogamy occurred in shaded tussocks or inflorescences.

The germination of nassella tussock was also studied. The pattern of germination was found to be variable which suggested that the evolution of localized ecotypes could have occurred. Dormancy was found to be limited and to occur after fruit dispersal. The degree of dormancy varied between the experimental sites. Germination could be enhanced by leaching fruits in running water for a few days. This and a simple bioassay suggested the presence of an inhibitor or complex of inhibitors, probably located in the lemma and palea. Reports that burning enhanced the germination of nassella tussock could not be repeated by simulation in the laboratory.

Nassella tussock was found to have a limited distribution. This was thought to be controlled mainly by the state of the vegetation. Nassella tussock is, however, adapted to the climate of the south-western Cape.

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Finally my wife, Margot, for her faith, support and patience and my son Kevin, who makes all the work worthwhile.

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PLATE 1.1: A small but mature nassella tussock (left) with enlarged flowering tillers and partly extended inflorescences. A ripe inflorescence is shown on the right. In the bottom left, from top to bottom are: a fruit enclosed in the glumes; the glumes; an intact fruit removed from the glumes and a naked caryopses (a fruit with the lemma and palea removed). Note the small size of the fruit. The sizes shown in this plate are approximately 75% of the true size.


10mm

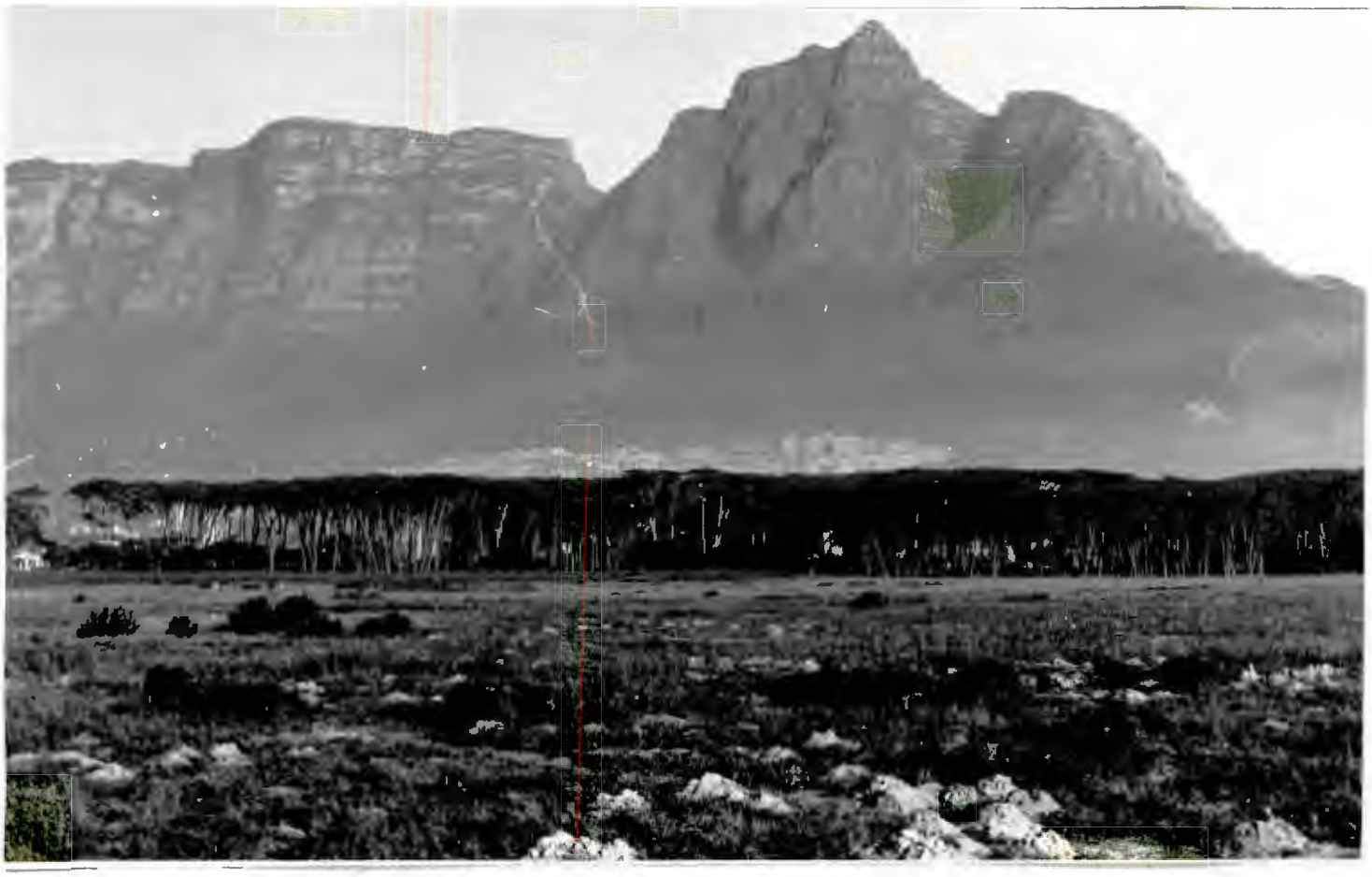


PLATE 1.2: A view of Devil's Peak, taken from the east. The University of Cape Town can be seen in the centre of the plate, with Rhodes Memorial to the right. Rhodes Estate is directly behind the University and extends up the slopes of Devil's Peak to just below the exposed rocky cliffs.

nassella tussock has been a physiological study of germination by Joubert (1981). Work on other Stipa species appears to have been carried out on the more important pasture species of the northern hemisphere. This work includes germination studies on S. capillata L., S. joannis Celak., S. rubens Smirn, and S. stenophylla Czern (Ovesnov and Ovesnov, 1970), S. viridula Trin (Dawson and Heinrich, 1952 in Ovesnov and Ovesnov, 1970) and S. bigeniculata Hughes (Hagan, 1976), seed set in S. falcata Hughes (Williams, 1963) and the autecology of S. nitida S. + H. (Osborn, 1931) and S. barbarta Desf. (Sankary, 1979). The effect of litter on the growth of S. thurberiana Piper was studied by Schlatterer and Tisdale (1969) while Langer (1972) states that S. comata Trin and Ruper is day neutral. Stipa species, recorded as being invasive in their native countries include S. brachychaeta Godr and S. tenuissima Trin. in Argentina, S. ichu Kunal in Peru and Bolivia and on a more local scale, S. filiculmis Del., S. filifolia Nees, S. laevissima Speg, and S. trichotoma (Wells, 1975). In South Africa S. tenuissima, along with nassella tussock is a declared noxious weed (Stirton, 1978).

1.1 GEOGRAPHICAL DISTRIBUTION

Nassella tussock, indigenous to South America has become established in Australia, New Zealand and South Africa, between latitudes 10 to 50° south (Wells, 1975). Nassella tussock has also been recorded from Tweedside in Scotland, Montpellier in France (Healy, 1945) and at five locations on the west coast of Italy (Moggi, 1971). There have been no reports of nassella tussock becoming weedy in the northern hemisphere. The highest concentration of the tussocks occur between 30 to 46° south and it is in this range that it becomes aggressively weedy. Wells (1973) indicates that the northerly distribution is

limited to cooler mountain ranges while in the south, lack of adequate rainfall becomes a limiting factor. Nassella tussock is described by Wells (1973) as a tolerant plant, thriving in a wide range of climate, soil and topographic conditions.

In its natural home in Argentina, nassella tussock appears to be limited to the humid pampas between latitudes 30 to 40° south and longitudes 48 to 67° west. This area is generally known as the grassland pampas and includes all of the Province of Buenos Aires, most of the Province of Cordoba and parts of San Luis, La Pampa and Santa Fe (Wells, 1973). Caro (Pers. Comm, in Zimmerman, 1972) notes that nassella tussock probably has two centres of distribution, namely the south and south western parts of the Province of Buenos Aires and the central part of Cordoba, approximately 700 km apart. Connor (1960) found that nassella tussock was present, but not abundant in Santa Fe and Entre Rios.

The Australian infestations are found in the Capital territory, on the central and southern tablelands of New South Wales and to a limited extent in Victoria and Tasmania. This covers a range from approximatly 35 to 42° south and 143 to 150° east. The major centres of nassella tussock are at Bathurst, Gunderoo and Jerongale, New South Wales (Wells, 1973).

New Zealand has extensive nassella tussock infestations. The largest infestations are found in Marlborough and North Canterbury, extending from the Waimakariri River in North Canterbury to the Wairau River in Marlborough although nassella tussock is found widely throughout New Zealand (Dingwall, 1969). Initially nassella tussock was thought to be confined to the South Island (Healy, 1945) but later, Dingwall (1969) mentioned scattered investations in the North Island.

In South Africa the nassella tussock infestation is centred in the Eastern Cape, around Cathcart, Bedford, Somerset East and Barkley East (Wells, 1978). This infestation covers about 25 000 hectares of which 1 000 hectares are densely infested, 4 000 moderately dense and 20 000 hectares with light scattered infestations (Wells, 1975). Smaller infestations are found at Swellendam, about 200 hectares (Healy, 1978) and on the East slope of Devil's Peak, in Cape Town, which covers approximately 450 hectares (Hall and Bulley, 1980). An isolated occurrence of nassella tussock is found on the farm Dwarsrivierhoek, near Stellenbosch. An outlier infestation is found on the krans-top line in the Graaff-Reinett area of the Southern Cape (Wells, 1974).

1.2 CLIMATE AND DISTRIBUTION

The apparent climatic requirements of nassella tussock are seen to reflect a broad degree of tolerance as it is found in six different climatic regions. These regions, based on Walter et al. (1975) are: tropical summer rainfall; sub-tropical arid to semi-arid zone; Mediterranean type with summer drought and winter rain; warm temperate; typical temperate; and the arid temperate areas. Of these, the tropical summer rainfall is common to both Argentinian and South African infested areas, the warm temperate climate is common to infested areas in South America, South Africa, Australia and New Zealand and the typical temperate climate is limited to New Zealand infestations. Mediterranean type climate regions are found in South Africa, Victoria (Australia), Italy and France. The occurrence of nassella tussock in Italy is reported to be limited (Moggi, 1971). Neither the Italian nor French localities of nassella tussock are aggressively invasive. Wells (1973) states that in Victoria, nassella tussock is limited to small infestations.

In South Africa the infestations in the Mediterranean type climate of the Western Cape are small, confined to 450 hectares after approximately 50 years of moderate control (Hall and Bulley, 1980). It appears, therefore, that nassella tussock favours a summer rainfall, temperate type of climate.

1.3 SOILS

The distribution of nassella tussock is not limited by soil types (Wells, 1973). In New Zealand it is found on podsolic and azonal soils derived from limestone, greywacke, schists, sandstone or mudstone. In Australia the situation is similar in that nassella tussock occurs on a wide range of soils. In South Africa, with the distribution possibly limited by other factors it is not possible to indicate any preferences that nassella tussock may have. The pH of soils on which nassella tussock is found varies between 5 and 7 (Wells, 1973).

There is no distinction in the literature as to water requirements for germination or establishment of nassella tussock. Healy (1945) states that summer drought favours nassella tussock but according to Walton et al. (1975) New Zealand has no true summer drought regions. However, Healy (1945) has used summer drought as a secondary factor saying that it causes early maturity of annual species which in turn checks the growth of longer-lived species and thereby leaving suitable areas for nassella tussock invasion. Rainfall figures range from about 400 to 1 500 mm per year (Dingwall, 1969; Healy, 1945). In South Africa nassella tussock has been found in hot moist conditions and even in almost water-logged soils (Wells, 1973). There is therefore no clear cut indication as to when nassella tussock requires higher or lower moisture levels.

1.4 GERMINATION AND ESTABLISHMENT

Nassella tussock is said to germinate mainly in spring and autumn but does continue to germinate throughout the year (Healy, 1945). Campbell (1965), however, found that germination occurs in autumn and winter. Healy (1945) gave water rather than temperature as the controlling factor for germination, stating that if water were available, then nassella tussock would germinate at any time of the year.

Under experimental conditions Joubert (1981) found that the optimum constant temperature for germination of naked caryopses (lemma and palea removed) was 28°C or an alternating cycle of 20 and 10°C. When intact fruits were used then germination could only be obtained using alternating temperatures. Joubert (1981) found little difference in the percentage germination when 2 mℓ or 8 mℓ distilled water (i.e. moistening or submerging) was used in 70 mm petri dishes. When using 25 naked caryopses per 70 mm petri dish with 2 pieces of filter paper, it was found that 3,0 mℓ of water gave the optimum germination. However, the range of germination between 2,0 and 8,0 mℓ water per petri dish was only 10%. Joubert (1981) concludes that not much moisture is required for the germination of naked caryopses. No data are available for the moisture requirements of intact nassella tussock fruits.

In areas of summer drought, from October to December, Healy (1945) found that there can be 100% mortality of seedlings due to desiccation. This only happens to the spring-germinated seedlings and not to the autumn-germinated seedlings. Healy (1945) later states that the dry, north west slopes are suited to nassella tussock invasion. This contradicts the previous statement of desiccation causing mortality and shows the apparent

conflict between the habitat-needs of germination and establishment and mature tussocks.

It would seem that nassella tussock is adapted to low rainfall (500 mm per year) regions with low competition. It must, however, receive its moisture during germination and early establishment.

1.5 GROWTH TO MATURITY

Healy (1945) found that nassella tussock growth rate was equivalent to or greater than indigenous tussocks. In its first eleven months of growth, folinge increased up to 700 mm in length. This figure varied depending on locality and could be as low as 100 mm per year (Healy, 1945). Campbell (1965) stated that nassella tussock is a comparatively slow grower from seed. When he compared the growth rate of nassella tussock with short rotation rye grass and Phalaris tuberosa L., he found that the growth rate of nassella tussock was markedly lower than these two species. The growth rate of mature tussocks was also found to be slow (Campbell, 1965).

1.6 PHENOLOGY

Healy (1945) found that spring sown seedlings could start flowering after 18 months, that is, during the following summer. Late summer to autumn sown seedlings could flower in the same year, after only 10 months growth. Under field conditions tussocks were found to commence flowering when between 18 months and three years old (Healy, 1945).

The commencement of flowering can first be detected during October and November when thicker than usual tillers appear (Campbell, 1960). The stages in the flowering

of nassella tussock are as follows: about two weeks after the appearance of the flowering tillers the flowering heads emerge from the sheath, all floral parts appear green; after about three weeks most panicles have extended and the glumes have turned purple; during the fourth week three purple anthers and feathery white stigmas emerge between the lemma and palea, nassella tussock is then in full flower. Fertilization is rapid and the anthers disappear within a week. After five weeks the flowering stalk elongates and the fruit has reached the milk stage, that is, when the fruit is crushed the contents appear as a milky liquid. Fruits reach their dough stage, that is, the contents of the fruit have a doughy consistency, in the sixth week and dispersal of the inflorescences begins around the tenth week (Campbell, 1960).

CHAPTER 2

METHODS

2.1 THE STUDY AREA

The area available for a study site was a portion of Rhodes Estate which is situated on the lower slopes of Devil's Peak, near Cape Town. The Estate has a chiefly east aspect, is between 100 and 440 m above sea level and is about 450 ha in extent. State forest land borders the Estate to the north, west and south while the eastern side borders on the University of Cape Town and De Waal and Rhodes Drives.

Rhodes Estate is a well used tourist site and is frequented by many hikers and strollers. It is stocked with free roaming fallow deer and Himalayan barking deer. Mixed herds of horses and donkeys are frequently taken onto the Estate to graze. These activities have resulted in the degeneration of the Estate by overgrazing and erosion. This has played a role in the Estate becoming a prime area for the establishment of alien and invasive plant species.

The locality as well as the function of the Estate had to be taken into consideration when choosing experimental methods. The function of the Estate as an open public area meant that nassella tussock could easily be spread to surrounding areas. As a control programme has been underway, on a high key, since 1976, the experimental sub-sites were not to spread caryopses either via natural agents or man to other parts of the Estate or surrounding areas. This meant that experimental plots had to be fenced so as to keep man and animals out and to prevent the dispersal of mature inflorencences. Although control

of nassella tussock was first initiated in the mid 1930s, this was on a very low level. The control programme was intensified in 1976 and by December 1979 when most of the field plots were to be located and fenced, there were only limited suitable areas left for study. However, reasonably adequate coverage of the various habitats was achieved.

2.2 THE RELATIVE GROWTH RATE OF NASSELLA TUSSOCK ON RHODES ESTATE

The aim of this study was to investigate the relative growth rate of nassella tussock in the Mediterranean-type climate of the South-western Cape. However, the topography and vegetation of Rhodes Estate are diverse so that no one site could be selected as being truly representative of the whole Estate.

2.2.1 The Study Sites

The vegetation of the Estate is mainly made up of alien plants that have been planted deliberately. Large areas have been covered with stone pine (*Pinus pinea* Linn.), the steep gulleys are filled with a mixture of evergreen trees, including some indigenous species, while the ridges and exposed areas are under tussock grasses or a sward, mainly *Digitaria diversinervis* Stapf.

The topography of the Estate varies from gentle open slopes to steep densely wooded gulleys. The slope variation of the Estate results in there being north and south aspects even though the general aspect is east. The higher, more inaccessible areas tend to be better vegetated than the lower, more publicly frequented zones. Selection of study sites was, therefore, based on aspect,

altitude, canopy cover (or exposure to sunlight) and the associated plant communities to give a representation of the major infested areas of the Estate.

Three study sites, each consisting of three sub-sites, were selected within the study area (Rhodes Estate). Each sub-site was four by four metres and enclosed with 1,2 m high chicken-mesh wire. Figure 2.1 shows the localities of the sites in relation to the topography and soils of Rhodes Estate.

The relevant data for the experimental sites are shown in Table 2.1. The sub-sites were located within a radius of 50 m except in site 1. Sub-site 1.3 was positioned 300 to 400 m north of sub-sites 1.1 and 1.2 (Figure 2.1). As a result, sub-site 1.3 had an east to north-east aspect, an altitude of 280 m, was more exposed to wind and received more direct sunlight than sub-sites 1.1 and 1.2 (cf. Table 2.1). Plate 2.1 shows sub-site 1.3 and sub-sites 1.1 and 1.2.

Site 2, located in a shallow valley, is shown in Plate 2.2 and the nature of site 3, under evergreen trees, is shown in Plate 2.3.

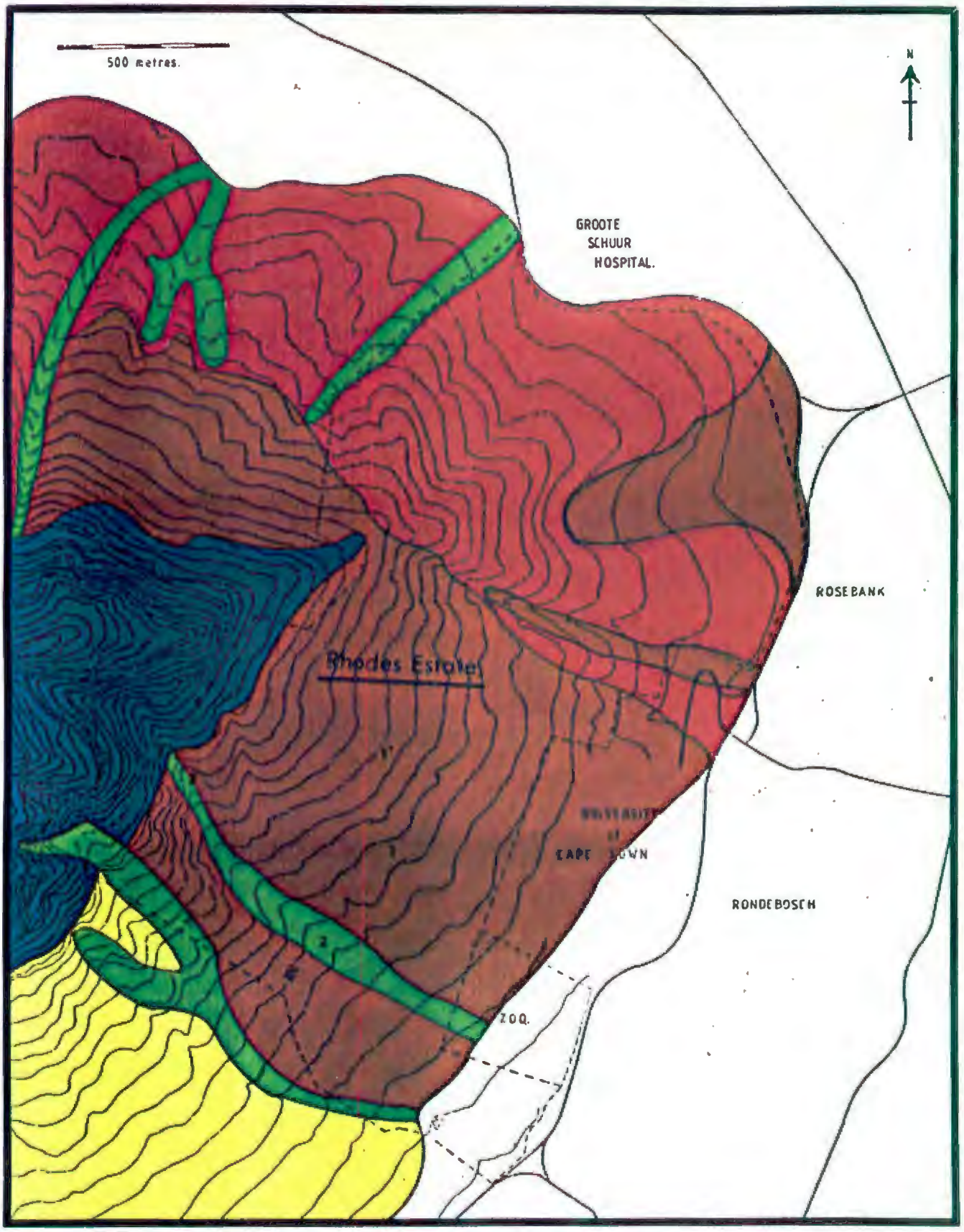


FIGURE 2.1: The topography and soils of Rhodes Estate. The location of the experimental sites are shown. 1, sub-site 1.1 and 1.2; 1, sub-site 1.3; 2, site 2 and 3, site 3.

TABLE 2.1: The relevant data of the sites used in the field experiment.

Site	1	2	3
Altitude	200 m	220 m	340 m
Aspect	East to South East	East to South East	South to South East
Slope	10°	10°	30-40°
Soil Assoc.	Zwartfontein/Trevanion/ Mispah	Jozini/Shorrocks	Jozini/Shorrocks
Soil depth	800-1200 mm	300-800 mm	300-800 mm
Stone frequency	Many	Many	Many
Stone size	20-100 mm	20-100 mm	20-100 mm
Extent of shading(1)	50%	zero	100%
Ground cover(2)	0	Dense tussock grass	0
Other vegetation(3)	*Pinus pinea* Linn.	Tussock grass	*Halleria lucida* Linn *Rapenaea melanophloeos* (L) Mez. *Maytenus* H.B.K. *Cassine*. L.

(1) Shading given here does not include that from Table Mountain and Devil's Peak. All sites experience shading from the mountain with site 3 receiving the most shade.

(2) Ground cover represents species in direct competition with nassella tussock.

(3) Other vegetation represents the plants of the community in which the site is located.

PLATE 2.1: Part A shows the location of sub-sites 1.1 and 1.2 in an open stand of stone pine trees.

Part B shows the location of site 1.3 in a more exposed area but still under stone pines.

Both pictures were taken at approximately 1100 hours on a clear sunny day in mid-August. Note the different degrees of shading between sub-sites 1.1 and 1.2 and sub-site 1.3.

A

B

PLATE 2.2: The locality of experimental site 2. The area has scattered shrubs but is mostly a tussock grassland. Large sandstone rocks are scattered across the area.

The picture was taken at approximately 1100 hours on a clear sunny day in mid-August. Note that there is only very limited shading (cf. Plates 2.1 and 2.3).

PLATE 2.3: The locality of experimental site 3. The area is on a steep south to south-east aspect with a moderate to heavy canopy. There is little ground cover other than nassella tussock.

The picture was taken at approximately 1100 hours on a clear sunny day in mid-August. The area was heavily shaded at this time and only gets broken sunlight for a short while at midday.

2.2.2 The Measurement of the Relative Growth Rate

The usual methods used to monitor the growth rate of grasses include tiller production, the increase in the number of leaves, leaf mass and biomass. It was decided that none of these methods were suitable for this experiment. It was not feasible to monitor either tiller or leaf production because of the shortness of the tillers and the high numbers of leaves and tillers produced in a tussock. The limited number of available tussocks, as a result of the control programme, put a restriction on the use of destructive sampling methods. Criteria that have previously been used to describe the size of nassella tussocks are the length of the longest leaf and the diameter of the tussock base (Healy, 1945).

The length of the longest leaf and the diameter of the tussock base were chosen as being the most suitable methods for monitoring the relative growth rate of nassella tussock on Rhodes Estate. The length of the longest leaf was taken as the length of the longest green leaf at the time of measuring. Measurements were taken using a wooden carpenter's ruler, with the ruler always placed between the tussock and its wooden identity marker. The ruler was placed near the marking tag so as to limit error due to the slope of the ground and erosion or depositions of soil around the base of the tussock.

Basal diameter was measured with a micrometer. This was found to be unsuccessful due to the irregular shape of the tussock base. It was decided that the basal circumference of the tussock would be a better character than the diameter. The circumference was measured with the same carpenters ruler which was adapted with a piece of nylon coated trace wire (Plate 2.4). The wire was anchored at the high valued end of the ruler, in this case 50,0 cm, passed through an anchoring pin and then

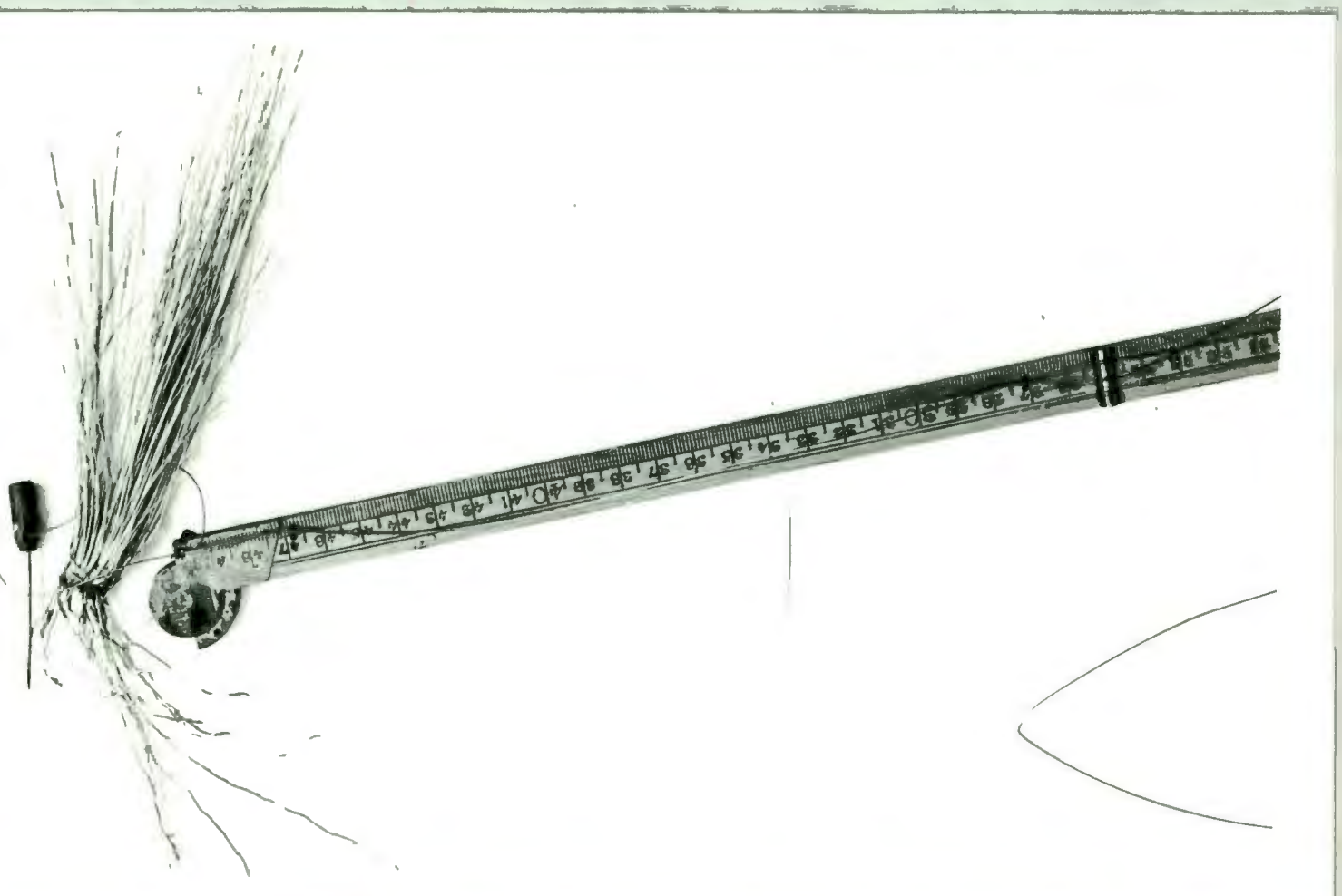


PLATE 2.4: The basal circumference measurer made from a wooden carpenter's ruler. The plate shows how the apparatus is used. The trace wire is placed around the tussock and held in place by the anchoring pin (seen on left of tussock). Once the tension is applied the diameter is read off the ruler. Note that tussocks were not uprooted for measuring as shown in this explanatory plate.

along the ruler to the 0,0 cm end. Retaining loops were placed at intervals along the ruler to hold the wire in place. The wire was then marked and calibrated so that when 1 kg tension was applied it registered 0,0 cm when empty. Basal circumference of a tussock was then measured by looping the wire around the tussock base, securing the far side of the loop through the running anchor pin and applying 1 kg tension to the wire by using a small fisherman's weighing scale. The basal circumference was then read off where the calibration mark coincided with the ruler's markings.

Each sub-site was marked into sixteen square metre quadrats. Four diagonal quadrats were used to represent the whole sub-site. Fifty tussocks per sub-site were selected randomly and marked with wooden dowel markers. These tussocks were then monitored monthly for growth, using the two methods described above. The mean relative growth rate was calculated for each sub-site and used to compare the relative growth rate within and between the three sites.

The relative growth rate (RGR) was computed from:

$$RGR = \frac{\frac{X_2 - X_1}{X_1}}{\Delta T}$$

RGR = Relative growth rate given in units of length (cm) or circumference (mm) per unit time (days).

X_1 = Length of longest leaf in cm or basal circumference, in mm, at time A.

X_2 = Length of the longest leaf, in cm, or basal circumference, in mm, at time B.

ΔT = Time in days between A and B.

2.3 PHENOLOGY

Phenological observations were undertaken both on the marked tussocks for studies of RGR and those scattered about the Estate. Many of the month-to-month observations on the condition of the tussocks were made while the RGR measurements were being taken. However, the intense monitoring of the flowering was carried out separately but using the marked tussocks.

Notes were made as each tussock initiated flowering and its progress to seed dispersal. The size of the tussock was noted when flowers were first seen. Any special ecological factors for each tussock were also noted. At the time of estimated fruit maturity, all the inflorescences were collected and placed in marked plastic bags. These were then air-dried, sealed and stored at 4°C. The inflorescences were then counted to estimate the number of inflorescences produced per tussock. The estimation of fruit production per tussock is a time consuming task. It was, therefore, decided to count the number of fruits produced in fifty tussocks and to use this mean as a representative figure for the production on the Estate.

2.4 GERMINATION

The germination of nassella tussock has previously been studied by Healy (1945) and Joubert (1981). The 'natural' rates of germination were generally found to be low. Increased rates were artificially achieved by removing the lemma and palea or by chemical stimuli (Joubert, 1981). In the present project the factors controlling the germination of nassella tussock caryopses were studied with special reference to field conditions in a Mediterranean-type climate.

2.4.1 Standard Techniques

The propagule of nassella tussock is, as in all grasses, a caryopsis. This is tightly enclosed in the lemma and palea and is usually incorrectly referred to as a seed. In this work the propagule will be used in most experiments and will be termed a fruit.

Before any experimentation could begin, the fruits had to be removed from the inflorescences and then sorted for apparent viability. The fruits were initially removed and sorted by hand but this proved to be too slow for the number of fruits that were required. It was found that a large Wiley Mill could be adapted to function in separating the fruits and inflorescences. With the blades at a gap of approximately 5 mm, whole inflorescences were fed into the mill. The fruits and remains of the inflorescences were separated by passing them through a 2,0 mm sieve and then by winnowing with an electric fan. Sorting for viable fruits was done with the aid of a bench top aspirator. The fruits were scattered on a white sorting board and the required fruits were collected with the aid of a plastic tube and vacuum, in a glass jar.

All the germination experiments were carried out on Whatman No. 1 filter paper in 90 mm glass petri dishes. Two pieces of filter paper covered the bottom of each, soaking in about 5 mℓ of distilled water. Distilled water was added as required to keep the filter paper fully moist throughout the experiment. Initially 50 fruits were placed in each petri dish. This number became exhaustive on the stock of fruits so finally 25 were used per dish. For each experiment four replicates were used.

All germination experiments were carried out in a Conviron Growth Chamber. The temperature régime used was 20°C and 10°C, day and night respectively. The light source

was by fluorescent and incandescent light with an intensity of 8 000 lux. The light regime used was 12 hours light with 12 hours dark. Experiments were normally terminated after 21 days except in special cases where the time may have been shortened to 10 days or lengthened as required. Where this has been done, the duration of the experiment will be discussed in those sections.

A fruit was classified as germinated once the coleorhiza and coleoptile could be seen with the naked eye. These could be seen as a furry white protrusion at the base of the fruit.

2.4.2 Standard Leaching

Various methods of leaching seeds or fruits have previously been used in attempts to enhance germination. Ovesnov and Ovesnov (1971) achieved increased germination by germinating seeds in sand in a glass tube through which water was passed. Landgraff and Juntilla (1979) used both running and standing water for leaching. Bewley and Black (1978) discussed the rapid loss of solution from fruits during the first 30 minutes of water uptake. They suggested that these solutes may stimulate germination as well as the growth of fungal pathogens in the soil. The extraction of inhibitors from seeds has been either by means of alcohol or water (Enu-Kwesi and Dumbroff, 1980; Goodchild and Walker, 1971; Martinez and Santos-Ruiz, 1978; and Murphy and Noland, 1981). From these studies it appears that by exposing seeds (sic) or fruits to excessive amounts of water one could wash the inhibitors away from the site of germination.

The method of leaching nassella tussock fruits was to enclose them in a chamber through which either tap or

distilled water was passed. Because of the poor wettability of the fruits, an open container could not be used as this would produce variations in the duration of actual leaching. The apparatus designed for leaching the fruits is shown in Plate 2.5. The apparatus was made from four plastic air flow taps, commonly used to regulate aeration in aquaria, and 7,0 mm inner diameter tubing. Leaching chambers, 80,0 mm long, were cut from this tube. One end was plugged with a 7,5 mm outer diameter tube which held a 15 by 15 mm piece of polyester mesh cloth in place. This narrow tube also served as an adaptor to fit the outlet of the tap. The opposite end of the leaching chamber was covered with a piece of polyester mesh cloth, held in place with a number one poly top pill vial lid. The top of the pill vial lid was removed to allow water to flow through. The fruits were placed in these chambers and the system was then connected to a water outlet and leached for four days. The water ascended through the chambers to allow the air to escape and to facilitate mixing of the fruits. The flow rate was approximately 2,5 litres per hour per chamber.

2.4.3 Alcohol Leaching

As discussed in section 2.4.2 inhibitors present in seeds (sic) are usually extracted with water or alcohol. Dormant seeds (sic) buried in the soil have been forced to germinate with an application of ethanol (Anon. 1981). The leaching experiments were extended to replace the water with different percentages of alcohol to determine what effect this would have on the germination of nassella tussock fruits.

The poor wettability of nassella tussock fruits was more critical in this experiment as the time factor involved was minutes, not days. The fruit leacher was adapted by using two taps and chambers. One tap and chamber was

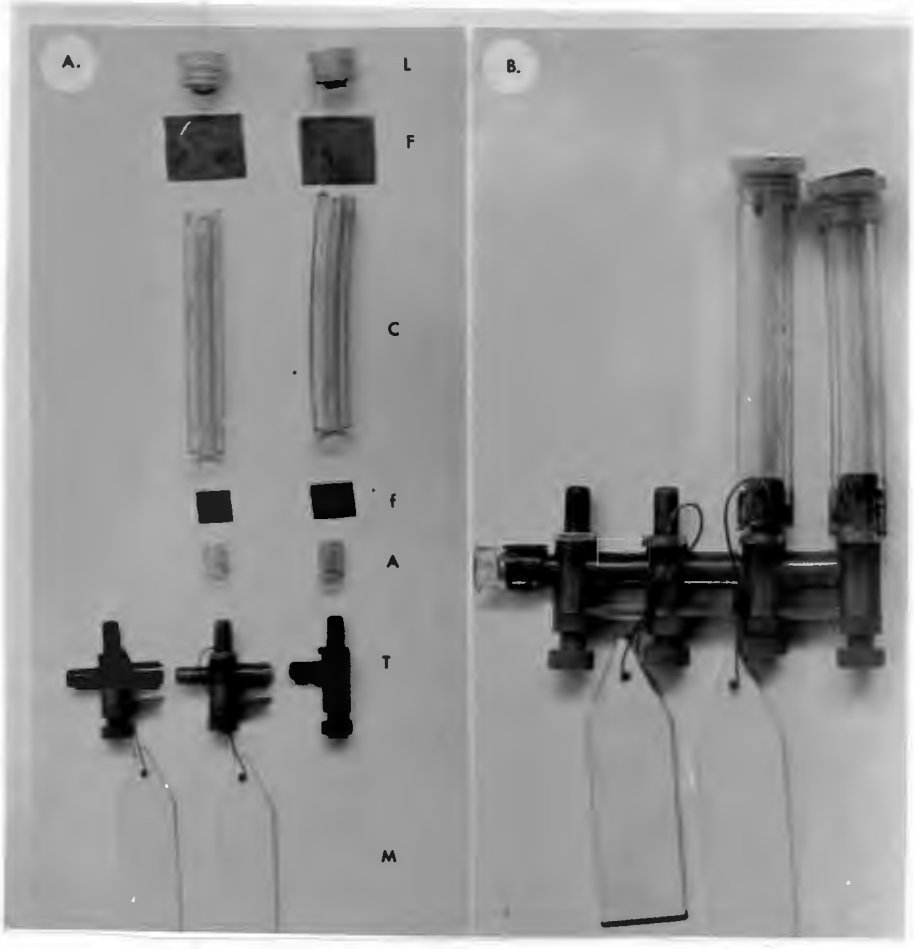


PLATE 2.5: The apparatus designed for leaching fruits.
(A.) An exploded view of the 'fruit leacher':

L - lid; F - end filter; C - leaching chamber;
f - first filter; A - adaptor; T - taps
M - marker tags.

(B.) The fruit leacher with two chambers constructed and in place. This plate (B) is about 50% of the true size.

turned through 180° so that there was an upper and a lower chamber (Plate 2.6). Fruits were placed in the lower chamber while the upper chamber served as an overflow reservoir. The inlet and outlet of the tap system was sealed so that fluid flow was restricted through the two chambers. The end of the fruit chamber was immersed in ethanol while suction was applied to the upper chamber. The ethanol was taken up, filled the fruit chamber and into the overflow reservoir. The ethanol was removed by blowing into the upper chamber. The fruits could be washed in distilled water without being removed from the chamber, simply by repeating the process using water in place of ethanol. This system allowed for rapid and complete removal of ethanol followed by immediate washing in distilled water so that the times of exposure could be precisely controlled.

Times of exposure to ethanol were 10, 15, 20, 30 and 60 minutes. The ethanol used was 25% and 50% (v/v). The fruits were then treated as discussed in section 2.4.1.

2.4.4 Exposure to Heat

Reports of prolific germination of nassella tussock after a burn (Denyer, pers. comm.) suggests that exposure to fire enhances the germination.

Nassella tussock inflorescences are not retained on the tussock once the fruits are ripe. Fruits, still in the inflorescence, can therefore be found lodged in other plants or windbreaks or lying on or buried in the soil. The effect of fire on nassella tussock fruits would then depend on the time of the burn in relation to the stage of the fruiting cycle. If the inflorescences are still attached to the tussock or lodged in some other obstacle then the fruits will be exposed directly to the fire.

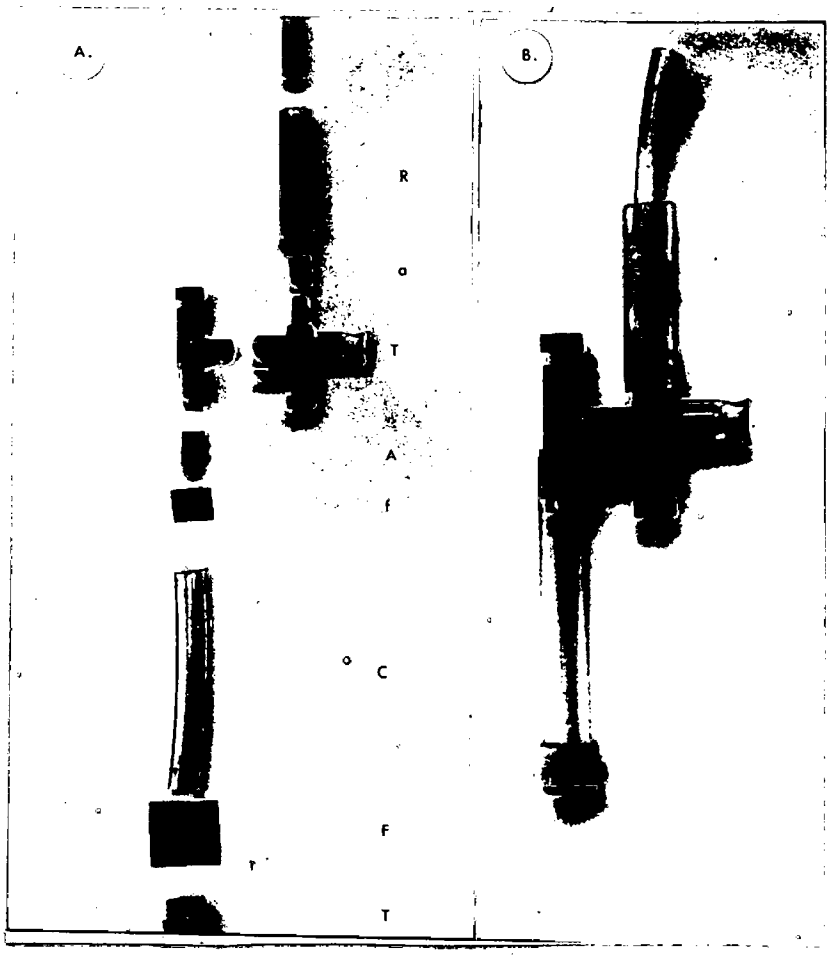


PLATE 2.6: The 'fruit leacher' adapted for alcohol leaching.
(A.) An exploded view of the modified leacher:

R - overflow reservoir; a - reservoir adaptor;
T - taps; A - adaptor; f - first filter;
C - fruit chamber; F - end filter and
T - top (or lid).

(B.) The constructed alcohol leacher. This is about 50% of the actual size.

Daubenmire (1968) quotes Pitot and Mason (1951) as giving the following temperatures at various heights above the ground in a grass burn:

0,0 m	90 - 140°C
0,5 m	285 - 560°C
1,4 m	140 - 375°C

However, they found that no temperature above 200°C was monitored for more than one minute while at the soil surface temperatures of more than 50°C were maintained for one to three minutes.

Those fruits that are buried are likely to experience different conditions during a burn. The most important difference is that the temperatures will be lower but the raised temperatures will be maintained for a longer period. Furthermore, the atmosphere around the fruits, during the burn, is likely to be more moist or humid than that above the ground.

The following experiments were carried out in an attempt to determine the effect of fire on both buried and exposed fruits.

2.4.4.1 Dry Heat

As nassella tussock fruits would most likely be found up to a height of 0,5 m above the ground the expected temperatures would be from 90°C to 560°C (Pitot and Mason, 1951). The effect of fire on the above ground fruits was simulated with a muffle furnace. Fruits were placed in the furnace at different temperatures for the required periods of time. The temperatures and times of exposure were as follows:

100°C for 60 seconds
200°C for 60 seconds
300°C for 30 seconds
400°C for 15 seconds

The fruits were then tested for germinability as described in section 2.4.1.

2.4.4.2 **Moist Heat**

In an attempt to simulate the effect of a burn on buried fruits, fruits were exposed to raised temperatures over a hot water bath. The water bath was covered with a sheet of expanded polystyrene so that a saturated atmosphere of steam could be created. Fruits were placed in polyester mesh bags and suspended below the polystyrene sheet, in the steam atmosphere (Martin and Cushwa, 1966).

The experiment was repeated with the fruits being placed on moist filter paper in petri dishes which were then floated on the water in the water bath. The bath was again covered with polystyrene to help maintain the temperature and saturated atmosphere.

The temperatures used were 50°C, 60°C, 65°C, 70°C, 75°C and 80°C. The duration of exposure to these temperatures was 10, 20, 30, 45 and 60 minutes. The fruits were then treated as described in section 2.4.1.

2.4.5 The Optimal Germination Temperature

Joubert (1981) determined that the optimal temperature for the germination of naked caryopses (fruits with the lemmas and paleas removed) of nassella tussock was a constant 28°C or an alternating temperature of 20°C and 10°C

for day and night respectively. It was necessary to determine whether the requirements of the fruits were similar to that of a naked caryopsis. No mention of the maximum and minimum temperatures at which nassella tussock would germinate could be found in the literature. While determining the optimal temperature for the germination of a fruit, the upper and lower temperature limits were also investigated.

A thermogradient bar was constructed, using Stein (1973) as a guide. An aluminium bar 1 000 x 150 x 25 mm was used. Heating of one end was supplied by a 60 watt spiral element and controlled by a 0 to 110°C thermostat. Cooling of the other end was achieved by using an alcohol cooling unit which circulated cooled alcohol through channels drilled in the bar. The bar was enclosed in a casing made from expanded polystyrene so as to isolate the surrounding atmosphere and insulate the bar to prevent heat exchange. Light was provided by a single 40 watt cool white fluorescent tube connected to a time switch. The surface of the bar was covered by three layers of Whatman No. 1 chromatography paper on which fruits were germinated. Distilled water was supplied via a small plastic tap and tube so that water was dripped onto the hot end of the bar at a rate of approximately 130 mℓ per hour. The temperature range obtainable was from 0 to 50°C with an accuracy of 0,5°C. A thermocouple, connected to a digital thermometer was used to monitor the temperature.

Fruits were placed on the bar, after four days leaching (section 2.4.2). The germinated fruits were counted and removed each day. The experiment was run for 35 days.

2.4.6 The Effect of the Removal of the Lemma and Palea

As discussed earlier, most of Joubert's (1981) work was carried out on naked caryopses, that is fruits without

the lemma and palea. Naked caryopses were used to compare the response of Rhodes Estate populations to those of the Eastern Cape. Naked caryopses were, in some cases, used as controls for other germination experiments.

The lemma and paleas were removed by gently rubbing the fruits between two pieces of wood (Joubert, 1981). The naked caryopses were then checked for damage and only undamaged ones were used in experiments.

2.4.7 Th Effect of Substrate on Germination

The limited nature of the nassella tussock population in the Mediterranean-type climate of the south-western Cape suggests that there may be special controlling factors there, limiting its spread. Healy (1978) indicated that the vast expanse of the Cape Flats may be ideal for nassella tussock. However, no nassella tussock has been found there. It is possible that the substrate has a role in the germination and establishment of the young tussocks.

Nassella tussock fruits were placed on different soil substrates to determine their effect on the germination. The soils were collected, air dried, sieved through 2,0 mm mesh sieve and then placed in petri dishes. The soils were moistened and the fruits scattered across the surface. Treatment was then continued as described for standard germination techniques (section 2.4.1).

The soils used in this experiment were collected from Rhodes Estate and the Cape Flats. The Rhodes Estate soil was collected on the 280 m contour, south east of site 3 (Figure 2.1). This soil consists of an oakleaf-Hutton association and is a brown medium-fine sand to sandy loam with a 7% clay content. The Cape Flats soil was collected from a site in Philippi. This site was a

clearing between Acacia trees and was probably used as a source for builders' sand. The Cape Flats soil is a coarse, white sand.

2.4.8 The Effect of Burial on Germination

Most of the seeds buried in the soil are found in the top 25 mm with few deeper than 100 mm (Harper, 1977). Nassella tussock has a high seed production with long viability (Healy, 1945) and can therefore be expected to have a large seed store in the soil. It is important to know whether these buried fruits contribute directly to the enlargement of a population or if they must first be brought to the soil surface before they will germinate.

A one centimetre layer of 2,0 mm sieved Rhodes Estate soil was placed in each of five plastic dishes. Each dish was then partitioned into three sections for replicates and 25 fruits scattered in each section. More soil was then added, giving the required depths of burial of 0, 1, 2, 3 and 4 centimetres. The soil was then moistened and the clear plastic lids of the dishes put in place. Treatment was then as described in section 2.4.1 except that germinated fruits could not be removed. In the buried samples, germination could only be recorded once the coleoptile had extended above the soil surface.

The experiment was repeated using Cape Flats sand.

2.4.9 Exposure of Fruits in the Field

The poor germination of nassella tussock and the methods employed by Joubert (1981) to enhance germination have been discussed in section 1.4. It is possible that fruits exposed in the field undergo degradation of the lemma and palea and thereby achieve greater levels of germination.

To experiment for this effect, fruits were exposed in the field, both on the soil surface and buried at a depth of approximately 40 mm.

Mesh envelopes, 100 x 100 mm were made from polyester mesh cloth. Fifty fruits were sealed into each envelope which was then anchored onto a cleared area of soil. The envelopes were grouped in three's for replication and a total of twelve groups were placed in the field.

Open topped boxes, constructed from the same polyester mesh cloth, were used for the fruit burial experiment. Fifty fruits were placed in each box and three boxes were placed in each of twelve groups. The top layer of soil, approximately 40 mm, was removed from the experimental site. The boxes, with fruits were then put in place and the surface soil replaced, burying the boxes. A nylon marker tag attached to each box was visible above the soil for later relocation.

Both these experiments were carried out on Rhodes Estate approximately 100 m due east of sub-site 1.3. Three envelopes and three boxes were retrieved bimonthly from the field. The fruits were removed, counted and it was noted whether germination had taken place or not. Any germination was expressed as a percentage of the number of retrieved fruits per sample. A sub-sample of each was subjected to the standard germination procedures (section 2.4.1). A further sub-sample was examined under the light and scanning electron microscope for damage to or degradation of the lemmas and paleas.

2.4.10 The Effect of the Absence of Light on Germination

The light requirements of nassella tussock naked caryopses is dealt with in detail by Joubert (1981). In this work

only the effect of total darkness on the germination of fruits was studied. This was done to determine whether the results obtained from germinating fruits buried at various depths (section 2.4.8) was caused by a lack of light. Healy (1945) found that fruits germinated readily in dense shade while Wells (1975) found little germination in heavily shaded areas. It was hoped that germinating fruits in total darkness would indicate their degree of germinability in dense shade.

Treatment of experimental material was as described in section 2.4.1 except for a few changes. Three pieces of filter paper instead of two, were used and about 7,5 mℓ distilled water was added per petri dish. The dishes, with fruits, were then sealed in dark cardboard boxes and placed in the Conviron Growth Chamber. Counting of germinated fruits was limited to the 21st day due to the limited availability of a dark counting area.

2.4.11 A Bioassay for the Presence of Germination Inhibitors in the Fruit

Joubert (1981) suggested that an inhibitor is present in the caryopses and that the lemma and palea restrict the leaching of this substance. The results obtained in the present work made it necessary to investigate further, the presence of an inhibitor in nassella tussock fruits. To do this, a simple bioassay using nassella tussock fruits and naked caryopses was undertaken.

.4.11.1 Extraction of Inhibitors and Chromatographic Separation

The method of extraction and separation of inhibitors has been adopted from Walker (1971) and Goodchild and Walker (1971). Walker (1971) discussed the suitability of the method for preliminary studies on inhibitors.

Goodchild and Walker (1971) used it on Trifolium subterraneum Linn. when working on methods for measuring seed germination.

Four grams of nassella tussock caryopses were ground with a mortar and pestle in 50 mℓ of 80% ethanol for 10 minutes. The liquid and resident were transferred to an Erlennmeyer flask, covered and stored at 4°C for one hour. The mixture was shaken periodically. After storage the liquid was double filtered through Whatman No. 1 filter paper. The filtrate was then vacuum evaporated at 35°C until the volume had been reduced to 10 mℓ. This was then partitioned three times with ethyl acetate. The ethyl acetate fractions were combined and reduced under vacuum to about 2 mℓ. This sample was then stored at 4°C.

The 2 mℓ sample was then strip loaded onto Whatman No. 1 chromatography paper. The solvent used was isopropanol: ammonia: water (10:1:1, v:v). A blank, using only solvent, was run, which was to be used as a control. The chromatogram was run descending for 10 hours or until the solvent front had travelled 30 cm from the start. The temperature of the room during this period was 20°C. The solvent front was marked, the paper dried at 30°C and then marked and cut into 10 strips of equal size, between the origin and solvent front (or 10 Rf strips). The strips were then cut into three 100 mm pieces and placed in marked petri dishes. Twenty-five naked caryopses were placed on the paper in each dish and 4 mℓ of distilled water was added. A sample of the control chromatogram was placed in 10 dishes to serve as a control. The treatment was then continued as described in Section 2.4.1.

2.4.11.2 Further Simplification of the Bioassay

Martinez-Honduvilla and Santos-Ruiz (1978) extracted inhibitors from pine seed coats using only distilled water.

Inhibitor activity has also been investigated by germinating seeds on the filtrate of crushed fruits (Mott, 1974).

In this experiment fruits were ground in 20 mℓ distilled water and then left to soak at 4°C for 24 hours. This was then double filtered through Whatman No. 1 filter paper and stored at 4°C. This process was repeated using only lemmas and paleas which had been separated from the caryopses. These filtered liquids were then used as the germination fluid for both leached fruits and naked caryopses. The germination procedure was, in all other respects, as described in Section 2.4.1.

2.4.12 Comparisons between Fruits of Different Colours and Shapes

Differences in the shape and colour of fruits were noticed within and between samples. The different colour and shape forms were separated with the aid of a dissecting microscope, leached for four days and then germinated as described in Section 2.4.1.

This is the only experiment in which sorting of the fruits, other than for apparent viability, was undertaken. In all other sections of this work, the mixture of shapes and colours, as found in that sample, was used for the particular experiment.

2.4.13 Comparison of Germinability of Fruits from Thomas River, East Cape and Rhodes Estate

The Eastern Cape populations of nassella tussock are found in an area with a warm temperate to tropical summer rainfall type climate. As has been stated previously the climate of Rhodes Estate is a Mediterranean-type with summer drought and winter rain. This experiment was

carried out to determine if there was any difference in germination between fruits from these two climatic regions.

Thomas River, located at 32° 31' S and 27° 15' E, is in the Cathcart District of the Eastern Cape. Fruits from this region were collected in November 1979 and 1980. The Rhodes Estate fruits were collected in November 1980. All fruits were stored at 4°C until used. Samples were leached for four days and then germinated as described in Section 2.4.1.

2.5 RELATIVE GROWTH RATES OF NASSELLA TUSSOCK UNDER SEMI-CONTROLLED CONDITIONS

The study of the relative growth rate of nassella tussock in the field was carried out using non-destructive sampling methods (Section 2.2.2). The monitoring of relative growth rate under semi-controlled conditions was designed to supplement the field study in that it would make use of the more accurate criteria of biomass production. This experiment was carried out in the nursery of the University of Cape Town. The nursery borders on Rhodes Estate and is in an area where nassella tussock has become established. The area is therefore known to be suitable for the growth of nassella tussock.

The tussocks used were all germinated from caryopses fruits use in the germination experiments. Seedlings were removed from the growth chamber after two weeks. They were then hardened for a further two weeks in the laboratory before being transplanted to the nursery. The seedlings were planted in 4 ℓ plastic nursery bags, filled with soil from Rhodes Estate. This was the same soil as described in Section 2.4.7 and is an association of Oakleaf and Hutton forms. Four hundred and fifty seedlings were planted and then divided into three groups. One group

was placed under 70% shade-net, the other in a glass house to produce temperate conditions and the third remained in the open. Due to insufficient security, the conditions in the temperate glasshouse were not monitored. The conditions, however, consisted of raised temperatures and a considerably higher humidity than the outside atmosphere. All tussocks in the glasshouse were watered weekly by hand. The tussocks in the open and under 70% shade net were only watered if insufficient rains fell to keep the soil damp.

The relative growth rate was monitored bi-monthly. Five tussocks were collected per group, removed from the soil, washed and the roots separated from the rest of the tussock. The total root length was estimated using the grid method described by Newman (1966). Root length measurements were limited to small tussocks because after 6 months growth the root systems were too large to be measured by this system. The field parameters, leaf length and basal circumference were measured. The numbers of tillers and leaves were counted in the young tussocks. Once the tussocks reached approximately 100 tillers per plant then only tillers were counted.

The roots and aerial portions of the tussocks, still separate, were then oven dried at 80°C to constant weight. These samples were then weighed to give biomass production.

This experiment was also carried out with seedlings planted in Cape Flats sand. This was, however, limited due to difficulties in establishing the seedlings.

2.6 CLIMATOLOGICAL DATA

A comprehensive weather station was not constructed on Rhodes Estate because of the proximity of the station of the Geography Department on the University of Cape Town Campus. This station was used to supply rainfall and

temperature data. These data were supplemented by placing a thermohygrograph at both sites 1 and 3 (See map, Figure 2.1). These were placed in small Stevenson screens measuring 1 000 x 500 x 500 mm. These were constructed to stand about 100 mm above the soil so as to obtain data for the atmosphere relevant to nassella tussock. The thermohygrographs were positioned at these sites as it was felt that site 1 was most representative of most areas on the Estate infested with nassella tussock. ~~The thermohygrographs were positioned at these sites as it was felt that site 1 was most representative of most areas on the Estate infested with nassella tussock.~~ Site 3 represented the higher lying infestations. Site 3 was also chosen due to its difference from the other experimental sites.

CHAPTER 3

DISTRIBUTION OF NASSELLA TUSSOCK IN THE WESTERN CAPE

The distribution of nassella tussock to be discussed here is to be limited to that found in the summer drought-winter rain region of the Western Cape. Wells (1973) and Healy (1978) both give detailed findings of the distribution of nasella tussock throughout South Africa.

In the Western Cape there are two main points of nassella tussock distribution. The first found was near Swellendam, approximately 200 km due east of Cape Town. This infestation is not covered in this work as it does not fall within the summer drought-winter rain region of the Western Cape. The second major infestation is that on Rhodes Estate, Cape Town. This population is evidently approximately 50 years old (Hall and Bulley, 1980). It has produced some outlier populations in the immediate surroundings. Another small population, which possibly spread from Rhodes Estate, is found on the farm Dwarsrivierhoek in the Banhoek area, east of Stellenbosch.

3.1 RHODES ESTATE AND SURROUNDING AREAS

3.1.1 Rhodes Estate

Nassella tussock still occurs in most areas of Rhodes Estate even though control has been carried out intermittently since the mid 1930s. The density of infestations differs from one area to the next, with open areas having the least tussocks. Many mature tussocks are found in inaccessible

areas. With a clearing programme in progress no distribution map of the tussocks remains accurate. As clearing progresses some areas change from high density infestations to apparently uninfested areas, although the seed store may remain large. In other areas the plant density may increase, after control clearing, due to regrowth from the fruit store in the soil. There are, therefore, two populations: the plant population and the fruit population. This account, however, will be limited to the plant population as a study of the fruit distribution on Rhodes Estate would not have been feasible due to the small size of the fruits and the size of the area involved.

The distribution of nassella tussock on Rhodes Estate is essentially unchanged from that given by Hall and Bulley (1980). The one factor that has possibly changed is the age of the tussocks in the infested areas. Many of the areas which were covered by mature tussocks are now infested with young seedlings, many of which have not reached reproductive maturity. The results given in this section will be mainly a discussion of the effect of control and present distribution.

At present, Rhodes Estate can be divided into four categories, depending on the age and density of nassella tussock and the effectiveness of control. The first two categories are based on the state of the ground cover. The light brown area in Figure 3.1 has a broken ground cover mainly as a result of the large fallow deer population and over exploitation by man. The area was heavily infested with nassella tussock (Hall and Bulley, 1980) but has been substantially cleared. However, the area still has scattered tussocks of all sizes and would be rated as a heavy infestation by Healy's (1945) classification of infestations. The grey area (Figure 3.1) represents those areas less frequently visited by man and less severely

tramped by the fallow deer. As a result, the ground cover is heavier and the occurrence of nasella tussock is generally lower. This area has few scattered tussocks, most of which are mature. The lower portion of the grey blue area, that is the north east end of Rhodes Estate, is divided and fenced into camps. These camps hold controlled numbers of large buck and have a good ground cover. Only occasional scattered tussocks have been found there.

Within both these major divisions are two further sub-divisions. In Figure 3.1 the red areas represent localities with dense stands of mature tussocks. These areas have not been cleared for some time and have grown to include many reproductively mature tussocks. The density ranges from tussock leaves touching to approximately one per 10 m^2. The final category is those areas that have been cleared recently but have since shown strong regrowth from the fruit store (dark brown area, Figure 3.1). These areas were cleared approximately one year previously and now may have as many as 100 seedlings per m^2. This has occurred mainly in exposed areas that were previously heavily infested. In these situations, once nassella tussock is removed, there is very little other vegetation remaining. The buried nassella tussock caryopses appear to provide the first seedlings to become established.

3.1.2 Known Occurrence Beyond Rhodes Estate

The locality of Rhodes Estate and the likelihood of fruit dispersal from there to the surrounding areas has been discussed by Healy (1978) and Hall and Bulley (1980). The fact that this has occurred is shown in Figure 3.1 by the distribution of nassella tussock beyond the Estate. From this Figure it appears that two factors have been instrumental in the dispersal of nassella tussock. The tussocks found to the north of the Estate have probably

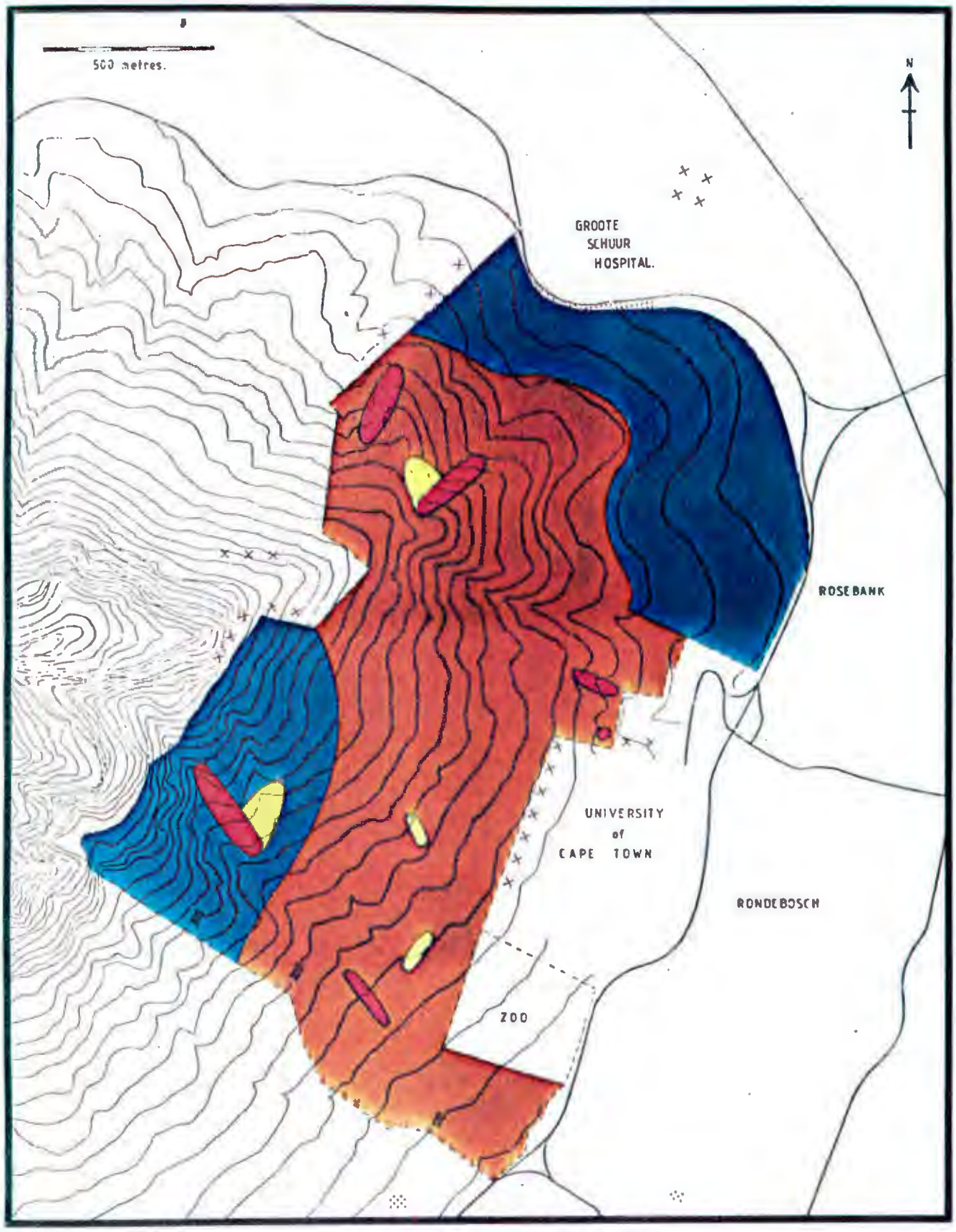


FIGURE 3.1: The distribution of nassella tussock on Rhodes Estate, showing the degree of infestation rather than actual numbers of plants. Crosses show known localities beyond the Estate. The areas of dots show previous localities that now appear to be controlled.

become established from fruit transported on the predominant south east wind which blows in the area during the months of dispersal, that is December to February. Fruit or whole inflorescences, carried in runoff water from the Estate during the winter rains are the most likely source from which the tussocks found on the Campus of the University of Cape Town became established. Scattered tussocks that have been recorded in the suburb of Rondebosch (Figure 3.1) became established after a washaway of a dam site on the Estate (Hall and Bulley, 1980).

In Figure 3.1 the dots indicate areas where nasella tussock have has been recorded but now appear to be under control. The crosses mark areas where mature, flowering tussocks are still found. The occurrence of nassella tussock in the Devils Peak Forest area to the north and north west of the Estate is limited. This area has only a few, scattered tussocks in spite of the fact that it may receive vast numbers of wind-borne fruits. The most likely reason for this is the heavier ground cover and more intensive management. However, portions of this reserve were severely burnt in March 1982 and this could well alter the balance in favour of nassella tussock.

A few tussocks are found to the west of the Estate, higher up the slopes of Devils Peak. As these are found on the margins of footpaths that are often reached from the Estate, it is most likely that these tussocks originated from fruits carried there by hikers. A single, mature tussock has been found on the northern slopes of Devil's Peak about one kilometre west of the lookout area at the end of Tafelberg Road. This tussock was found on the roadside and in a drainage ditch leading off the mountain. Although no other tussocks were found in the area this does show the possibilities for the spread of nassella tussock. This area was also burnt in March, 1982.

The tussocks found in Newlands Forest, to the south and along De Waal Drive, to the north (dots, Figure 3.1), are at present being kept under control. Most of the tussocks on the University of Cape Town Campus have been removed, except for a few in the northern corner of the property. The area shown to the north east of Groote Schuur Hospital is a brick field where approximately 30 mature tussocks are found. No control has been exercised in this area.

3.1.3 Possible Areas of Occurrence Beyond Rhodes Estate

Rhodes Estate has a large run-off of water during winter rains. The rains start about three months after the inflorescences have been shed from the tussocks. Although no observations were made, large numbers of fruits may be carried in this run-off water. Most of the water is either channelled directly into the city's drainage system or into two storage dams. The storage dams are used for irrigation while most of the water in the drainage system leads to the Liesbeek or Black Rivers.

Where possible the areas where this water is used, e.g. the University grounds and Rhodes Estate nursery, surveys were carried out to determine whether nassella tussock was present. The banks of both the Liesbeek and Black Rivers were also surveyed for nassella tussock. Nassella tussock was not found in any of these areas. This is most likely due to the heavy plant growth in these areas which is preventing nassella tussock from becoming established.

Healy (1978) suggested that the vast areas of the Cape Flats to ~~be~~ the east and south east of Rhodes Estate are suitable for nassella tussock. Although only a rudimentary search was undertaken, no nassella tussock was found. Weed inspectors and botanists working in the area have not found nassella tussock on the Flats. However, from this brief

survey and results of work to be discussed later, it is felt that it is unlikely that nassella tussock will become established on the Cape Flats.

3.2 BANHOEK

Nassella tussock was found on the farm Dwarsrivierhoek, in the Banhoek area in 1979. This appears to be an isolated infestation numbering about one hundred flowering tussocks and as many seedlings in 1980. A brief search in likely localities in the nearby regions revealed no further infestations.

The origin of nassella tussock in the area is open to speculation. The farm holds stocks of sheep and it is possible that infested fodder introduced the fruits as was probably the case on Rhodes Estate. However, the owner of the farm is a conservationist and botanist and is visited regularly by persons who would also have visited Rhodes Estate. It is, therefore, possible that fruits were introduced directly from Rhodes Estate.

The locality is somewhat unusual in that the ground cover, at present, is substantial with dense, thick grass. This will be holding the population in check. The area is also fairly heavily shaded, with many of the tussocks growing in a peach orchard. Although Wells (1973) states that nassella tussock has no soil preference, the soil of Rhodes Estate and Dwarsrivierhoek are similar. Both are dark brown, fine soils. No detailed soil analyses were carried out.

Much of the infestation is on the banks of drainage ditches which flow regularly in winter. These ditches eventually flow into the Breede river. This means that there is a

possibility that nassella tussock has, or may, spread downstream along the river banks and into irrigation schemes.

3.3 DISCUSSION

Nassella tussock has a relatively long history on Rhodes Estate but has spread only minimally from this point. This follows the pattern that is found in Mediterranean-type climates in Australia and Europe (see Section 1.2). From these distribution results and distribution data in the literature (Moggi, 1971 and Wells, 1973) it would appear that nassella tussock is not fully adapted to a summer drought-winter rain climate.

CHAPTER 4

THE RELATIVE GROWTH RATE OF NASSELLA TUSSOCK ON RHODES ESTATE

The relative growth rate measurements were started in April 1980. The length of the longest leaf was initially measured with a flexible steel tape but a carpenter's ruler, as described in Section 2.2.2 was used from May 1980. In April 1980 the basal diameter was measured with vernier calipers. It was felt that these results were inaccurate due to the irregular shape of the tussock bases. Therefore, in May 1980, the basal circumference was measured using the ruler/loop apparatus described in Section 2.2.2. Longest leaf and basal circumference measurements were carried out consecutively and as far as possible every thirty days. This interval, however, varied because of the weather. It was impossible to measure the growth rate in the rain or wet weather because of the difficulty in recording the measurements on the field data sheets.

The longest leaf recordings were continued until November 1980 for site 1 and October 1980 for both sites 2 and 3. These were interrupted during flowering. A final recording was made in March 1981 for site 1 and sub-site 2.1. Two final recordings were made for site 3 in February and May 1981. The measurement of basal circumference was terminated in October 1980 for sites 2 and 3 and in November 1980 for site 1. The onset of flowering determined the date of termination for both the longest leaf and basal circumference measurements. The longest leaf measurements could not be made while inflorescences were extending above the leaves. The thicker flowering tillers introduced errors while the presence of inflorescences prevented the use of the

ruler/loop apparatus which limited the measurement of basal circumference.

4.1 THE RELATIVE GROWTH RATE AT SITE 1

Expressed in histogram form (Figure 4.1), the relative growth rate of site 1 can be seen to have two out-of-phase peaks. This graph records the relative growth rate from May 1980 to March 1981. Sub-site 1.1 had the highest initial growth rate but this decreased in June to about 50% of the May value. This then increased steadily to peak in October. The relative growth rate then decreased in November, but the difference between the October and November values remained insignificant at the 95% confidence limits. The relative growth rate for sub-site 1.3 showed an initial negative value. From this point it increased steadily to have a maximum value in October. The relative growth rate then decreased in November as in sub-site 1.1, to produce a value significantly different to that obtained in October. The results for sub-site 1.2 differed from both 1.1 and 1.2. The relative growth rate for this sub-site started with a positive value in May, decreased to about 50% in June and then increased in July. It then produced an inexplicable decreased in September. Sub-site 1.2 showed its peak growth rate in November, thereby producing the second of the out-of-phase peaks. There was, however, no significant difference between the growth rates of sub-site 1.2 in October and November.

The next recordings were only made in March 1981, after the completion of flowering. Figure 4.1 shows a steep and significant decrease in the relative growth rates of all three sub-sites from November 1980 to March 1981. It is probable that the growth rate for both sub-sites 1.1 and 1.3 decreased continually during the break in measuring

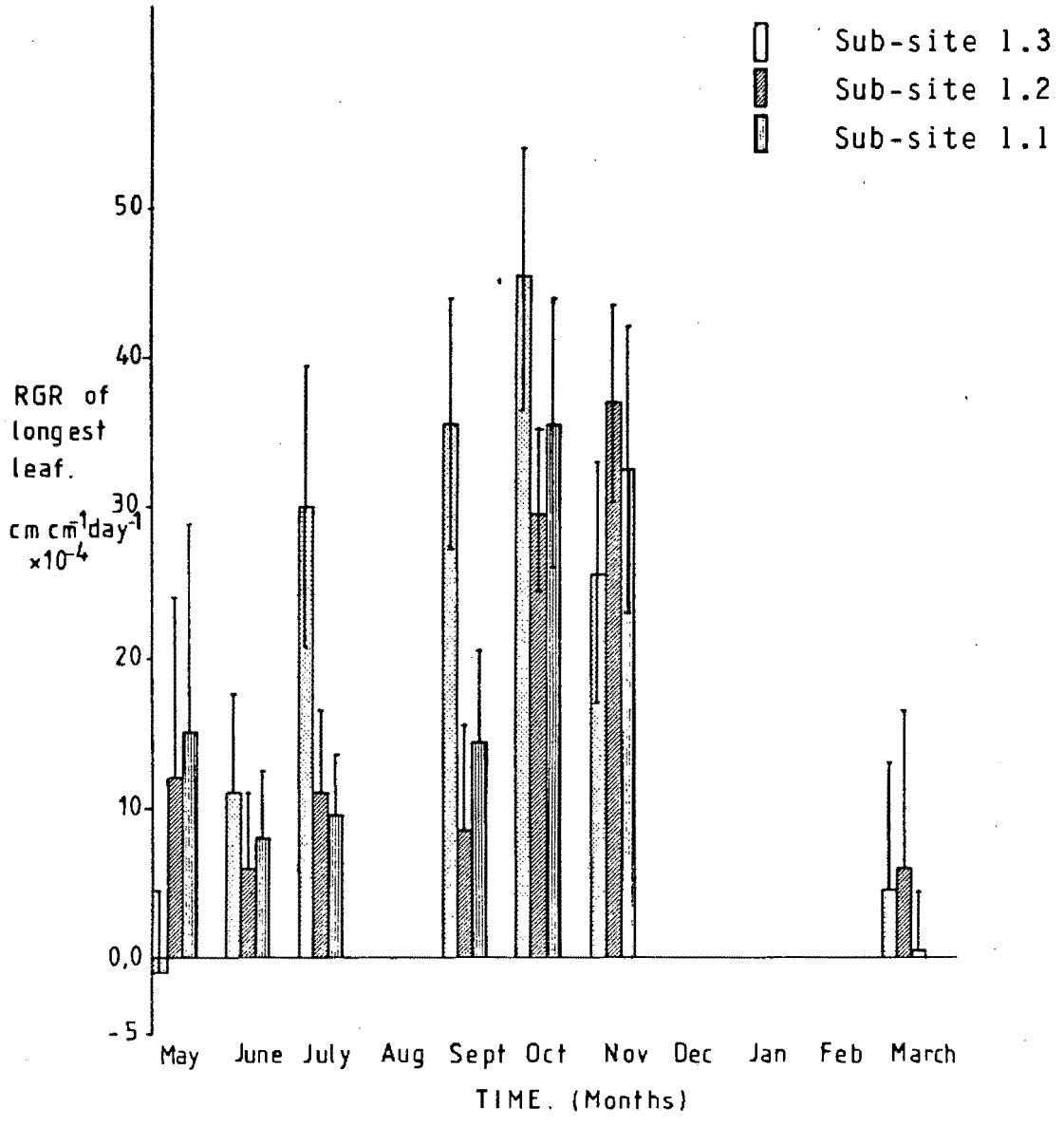


Figure 4.1: The relative growth rate of nassella tussock as recorded at site 1, Rhodes Estate, calculated from the length of the longest leaf. The experiment was conducted from April 1980 to March 1981.
The 95% confidence limits are shown.

from December 1980 to February 1981. This is assumed as both these sub-sites produced peak growth rates in October and started decreasing in November. This cannot be assumed for sub-site 1.2 as it only peaked in November. It is possible, but unlikely, that the growth rate for this sub-site increased in December 1980 before decreasing to the levels recorded in March, 1981. The visual appearance of the tussocks coincides with Figure 4.1, that is, that a continual decrease in the growth rate occurs from November through the flowering period. Once the inflorescences start to dry out the whole tussock deteriorates in condition and becomes dry and brittle.

The physical differences between the sub-sites of site 1 were discussed in Section 2.2.1. These differences are most likely responsible for the different trends, in relative growth rate, shown by sub-site 1.3 (Figure 4.1). Sub-site 1.3 showed a negative initial relative growth rate in May which then increased in June. Sub-sites 1.1 and 1.2 differed from this by having positive initial values in May with a decrease in rate in June. In July and September the relative growth rate was significantly higher in sub-site 1.3 than in 1.1 and 1.2. At no stage during the experiment, however, were the results from sub-sites 1.1 significantly different to those from 1.2. Sub-site 1.3 showed a significant decline in relative growth rate between the month it reached its maximum and the next month (i.e. between October and November). The difference found in sub-site 1.1 for the same period was insignificant. Sub-site 1.2 can not be compared in the same way as it produced maximum rates in November and no records were made in December.

Figure 4.2 shows the relative growth rate of site 1, calculated from the basal circumference data. The relative growth rate is expressed in $mm.mm^{-1}day^{-1}$ and the scale of the vertical axis has been changed to accommodate the higher values (cf. Figures 4.1 and 4.2). No values for May 1980

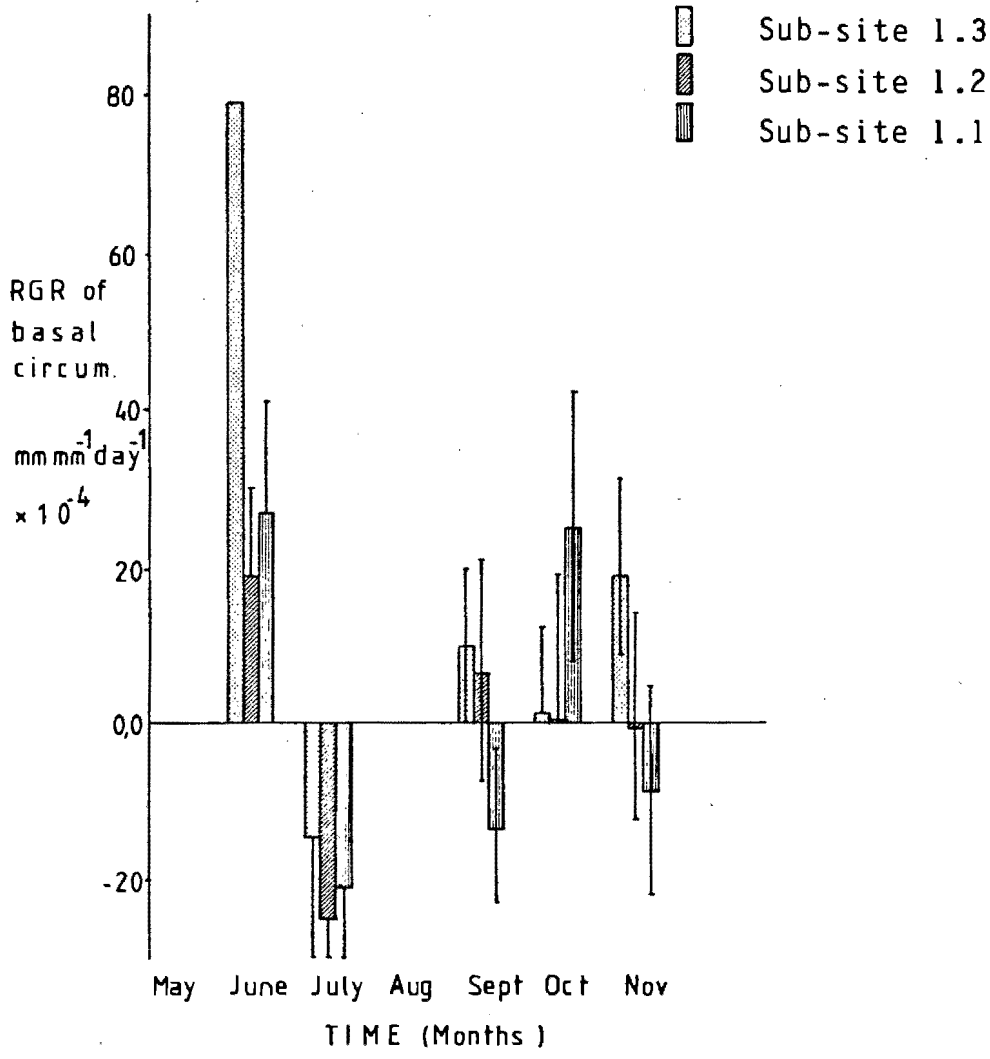


Figure 4.2: The relative growth rate of nassella tussock as recorded at site 1, Rhodes Estate, calculated from the basal circumference measurements. Note the change in the vertical axis to accommodate the higher growth rates. The 95% confidence limits are shown.

could be included as this was the month of transition from measuring basal diameter to basal circumference. No correlation can be found between the growth rate as measured by basal circumference and the longest leaf (cf. Figures 4.1 and 4.2). While the relative growth rate calculated from basal circumference is decreasing so the rate, calculated for the same period, from the longest leaf measurement, is increasing.

Although significant differences are recorded in Figure 4.2, these are so weakly correlated that they are of no value. Large negative values are common and while the rate for one sub-site is decreasing so that of another sub-site shows an increase of a similar magnitude.

4.2 THE RELATIVE GROWTH RATE AT SITE 2

The relative growth rate of site 2, calculated from the longest leaf data, is shown in Figure 4.3. The overall pattern of the relative growth rate is not dissimilar to that of site 1 (cf. Figures 4.1 and 4.3). All three sub-sites showed an increase in the relative growth rate from May to June and sub-site 2.2 continued this increase through to July. Sub-sites 2.1 and 2.3 have a decreased relative growth rate in July which then increased through September to peak in October. This decrease in rate from June to July was significant, at the 95% confidence limits, for sub-site 2.1. The October rates for sub-site 2.1 were also found to be significantly different from the September rates. Sub-site 2.2 differed from the above in that it showed a decrease in rate in September, followed by a significant increase in October. Only sub-site 2.1 was measured in November and this showed a significant decrease from the October values. Sub-sites 2.2 and 2.3 were not measured because of floral production.

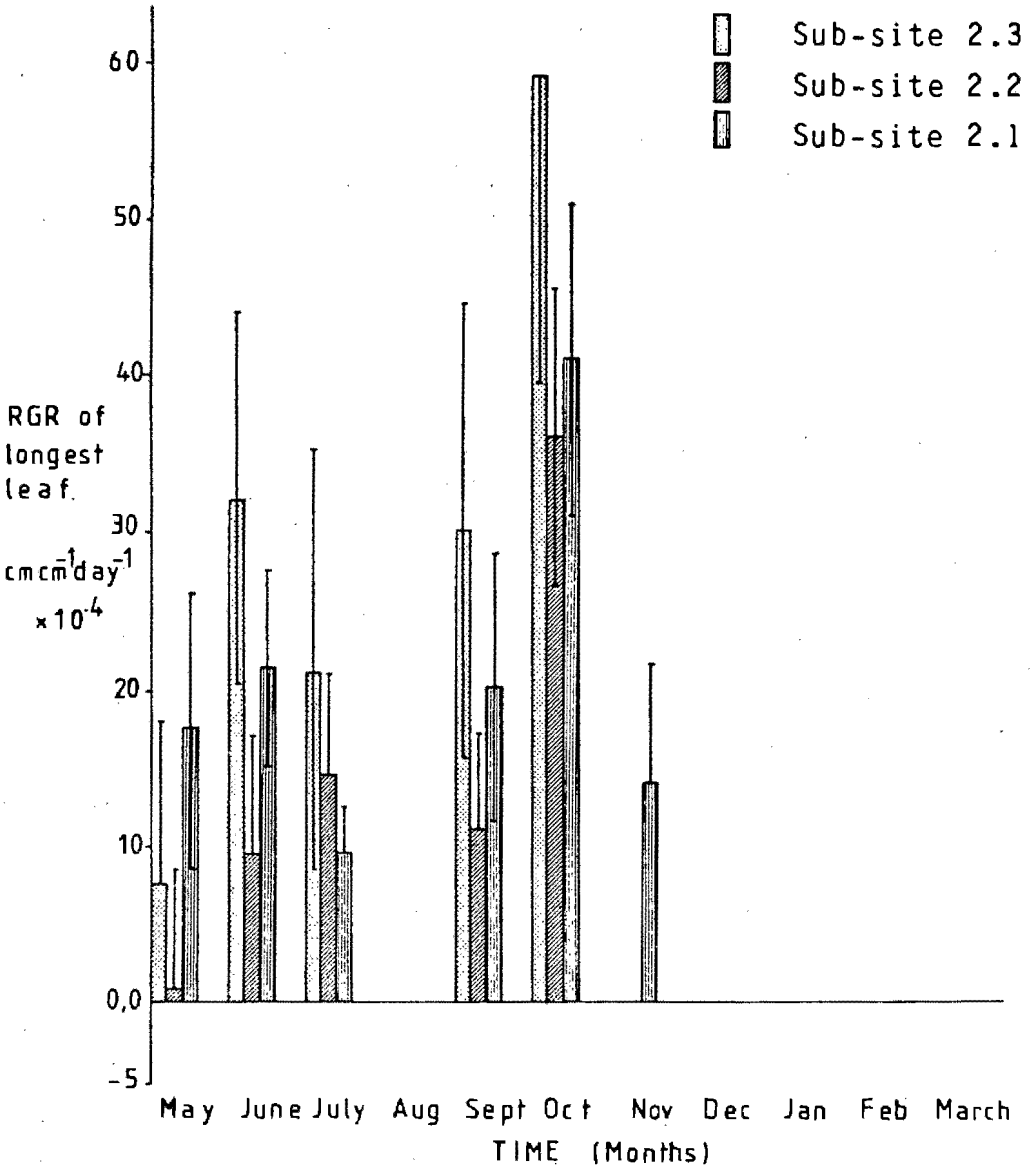


Figure 4.3 : The relative growth rate of nassella tussock as recorded at site 2, Rhodes Estate, calculated from the length of the longest leaf. The 95% confidence limits are shown.

At no time during the experimental period did any of the sub-sites show significantly different rates to both of the other sub-sites. In June sub-site 2.3 was significantly different from sub-site 2.2 but not from sub-site 2.1. There was no significant difference between sub-sites 2.1 and 2.2 at any time.

The relative growth rate of site 2, calculated from basal circumference data, is shown in Figure 4.4. As in site 1 (Figure 4.2) there are initial high rates of growth followed by steep decreases. Sub-site 2.1 decreased from $1,67 \times 10^{-2}$ $mm.mm.^{-1}day^{-1}$ in June to $-4,8 \times 10^{-3}$ $mm.mm^{-1}day^{-1}$ in July. The rates are irregular throughout the experimental period and no pattern of growth is evident.

4.3 THE RELATIVE GROWTH RATE AT SITE 3

The relative growth rate calculated from the longest leaf measurements of site 3 are shown in Figure 4.5. Both sub-sites 3.2 and 3.3 had negative rates for May and then increased in June. Sub-site 3.1 started with a positive value and decreased slightly in June but still maintained a positive rate. All three sub-sites decreased to negative values in September. Sub-site 3.3 started decreasing from June while sub-sites 3.1 and 3.2 increased from June to July before decreasing in September. The growth rates in October show an increase on the September rates but the values for sub-sites 3.2 and 3.3 remained negative. The low rates of growth being obtained resulted in a three month interval being left before the next measurements were made. A visual check was, however, maintained during this period of no measurements. In February 1981 sub-sites 3.1 and 3.2 showed steep increases in relative growth rates. The increase of rate in sub-site 3.3 was much lower. However, sub-site 3.2 was the only one to produce results in February 1981 significantly different to those for October 1980. The next measurements were made in

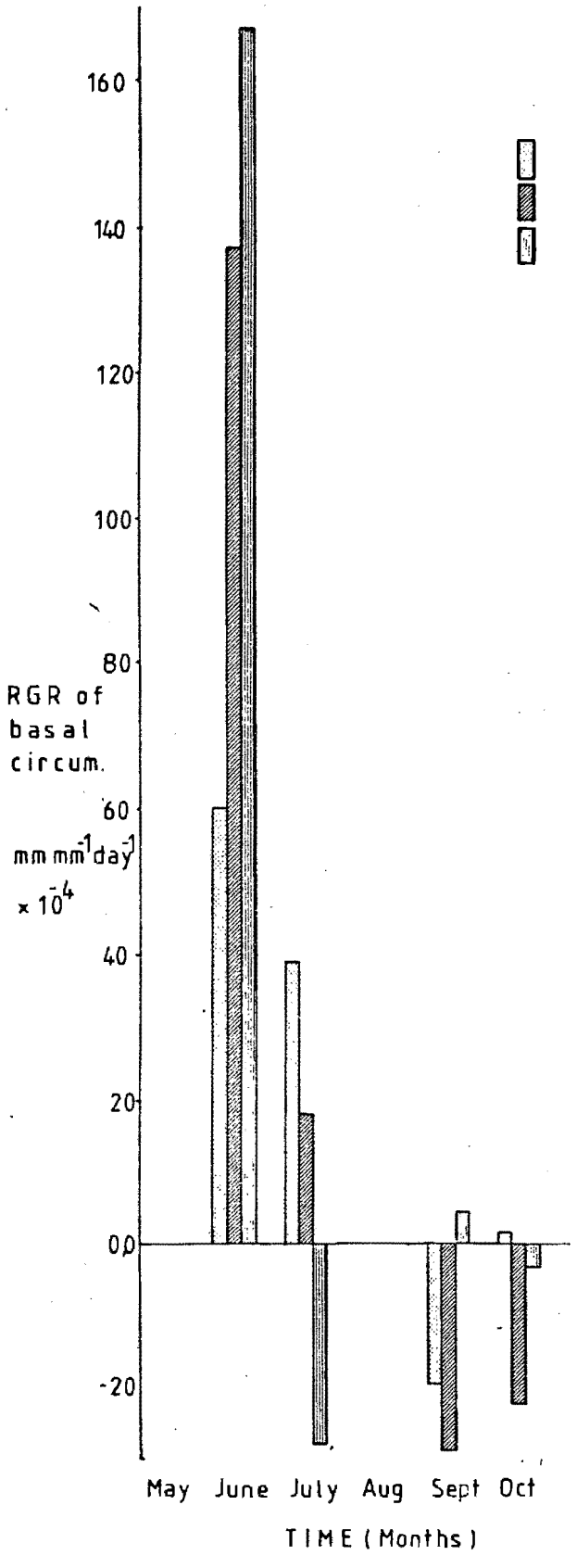


Figure 4.4: The relative growth rate of nassella tussock as recorded at site 2, Rhodes Estate, calculated from the basal circumference measurements. The 95% confidence limits are not shown because they are so large as to be of little significance.

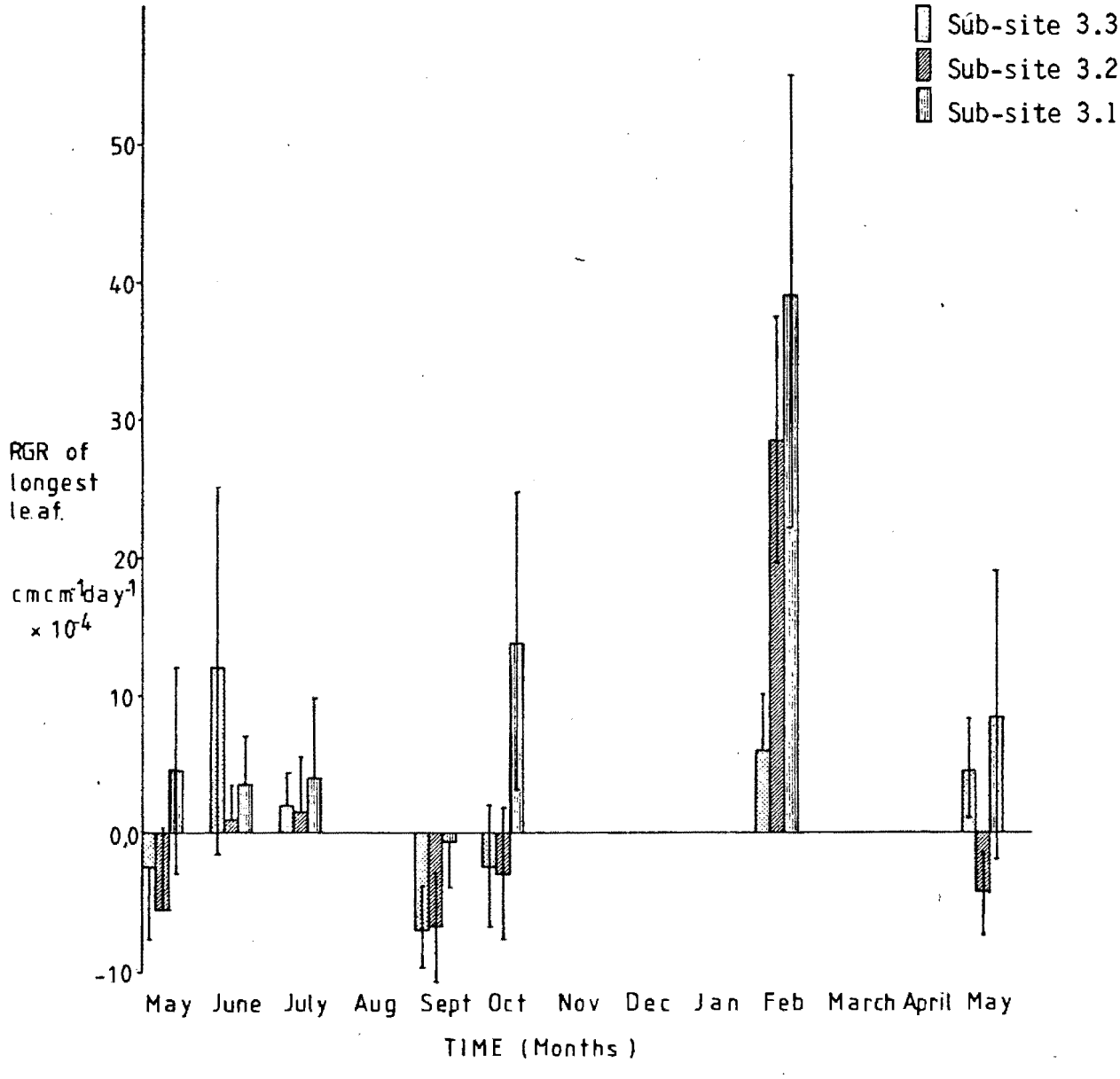


Figure 4.5: The relative growth rate of nassella tussock as recorded at site 3, Rhodes Estate, calculated from the length of the longest leaf. The experiment was run from April 1980 to May 1981.
The 95% confidence limits are shown.

May 1981, after the shedding of the mature inflorescences. These showed a marked decrease in rates with both sub-sites 3.1 and 3.2 producing significantly lower rates than those for February. The rates for sub-site 3.2 were negative. The rates for sub-site 3.3 were lower, but not significantly, than the February results.

The results of the growth rates calculated from the basal circumference data show a similar lack of pattern as was seen in Figures 4.2 and 4.4. The basal circumference growth rate for site 3 (Figure 4.6) shows significant decreases in rates from June to July but is not comparable to the pattern of growth shown in Figure 4.5.

4.4 SITE MEANS

The relative growth rates, calculated from the longest leaf data, are compared in Figure 4.7. These results are the means of the three sub-sites of each site.

When the results are expressed in this way the similarity between sites 1 and 2 becomes apparent. The magnitude of the growth rate of these two sites can be seen to be very similar except during June when site 2 showed higher rates than site 1. Both these sites had positive rates throughout the experimental period. The peak growth period for site 1 was October while site 2 appears to have peaked in October. However, the November rate shown in Figure 4.7 for site 2 is that of sub-site 2.1 only because sub-sites 2.2 and 2.3 were not measured. The overall growth rate of site 2 could, therefore, be different to that shown for November.

Site 3 shows a completely different pattern to both sites 1 and 2 (Figure 4.7). This site shows negative values in May and September and only in June was the growth rate

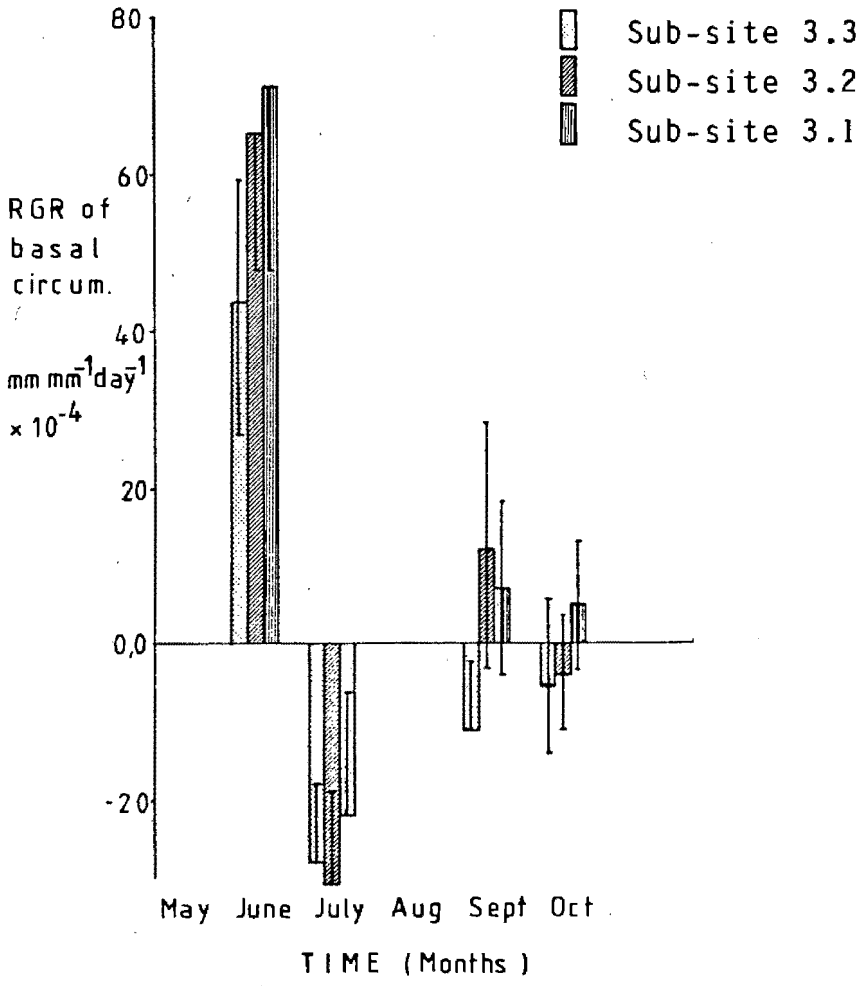


Figure 4.6: The relative growth rate of nassella tussock as recorded at site 3, Rhodes Estate, calculated from the basal circumference measurements.
The 95% confidence limits are shown.

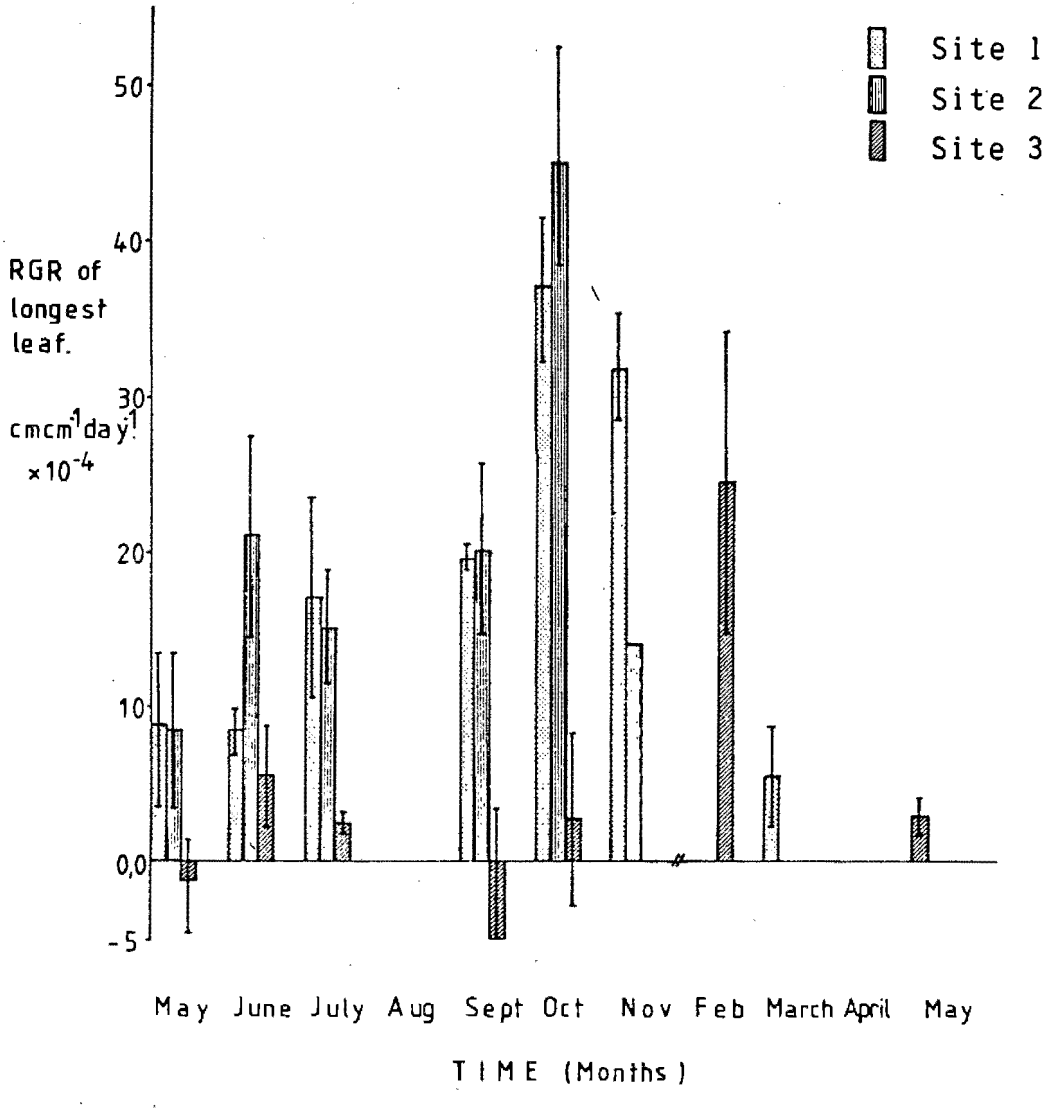


Figure 4.7: The mean relative growth rate of the three experimental sites calculated from the length of the longest leaf. Note that the November value for site 2 (broken vertical lines) is not a mean but the results from sub-site 2.1 only.
The limits shown are standard error, not 95% confidence limits.

similar to that of site 1. Throughout the year the growth rate of site 3 was in the order of 10^{-4}cm.cm^{-1}day^{-1} while that of sites 1 and 2 was mostly in the order of 10^{-3}cm.cm^{-1}day^{-1}. Only when site 3 shows its peak rate in February 1981 does it have a value of 10^{-3}cm.cm^{-1}day^{-1} and even then this is about 50% of the maximum rate of site 2. Site 3 has its maximum growth rate in February while sites 1 and 2 both peak in October and November respectively.

The mean relative growth rates of the three sites calculated from basal circumference are shown in Figure 4.8. This Figure is not dissimilar to any of the Figures on basal circumference shown for the separate sub-sites (Figures 4.2, 4.4 and 4.6). All three sites show large decreases from June to July with site 2 continuing to decrease through to September. Sites 1 and 3 showed increased rates from July to September. Sites 1 and 2 increased in October with site 3 decreasing slightly over the same period. This Figure shows no pattern of growth for the experimental period.

4.5 DISCUSSION

4.5.1 The Longest Leaf Measurements

From the results discussed in this chapter it would appear that the length of the longest leaf is a suitable criterion for monitoring the relative growth rate of nassella tussock. These results seem to have shown the month to month growth fluctuations as well as the seasonal peaks. However. the usefulness or accuracy of this method will not be discussed here. This will be dealt with in the next chapter, after it has been compared with biomass methods.

Using the length of the longest leaf to monitor growth is limited to the growth of the longest leaves only. The

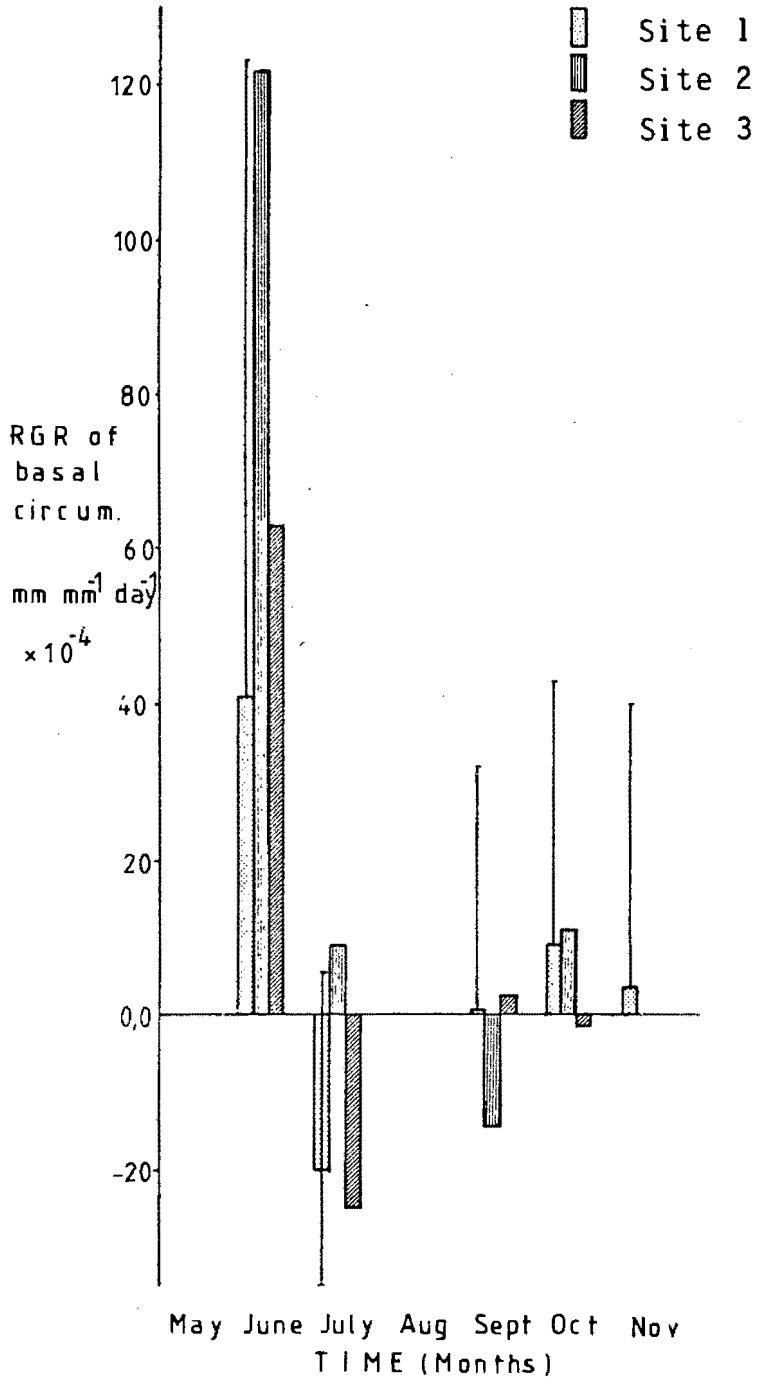


Figure 4.8: The mean relative growth rate of the three experimental sites calculated from the basal circumference measurements.
The limits shown are standard error, not 95% confidence limits.

leaf measured at time T_1 may not be the same leaf that will be measured at time T_2. Furthermore, the relative growth rate of the longest leaf or leaves may be totally different to that of very young shoots, which would not be recorded by this method. This method does not take into account the different processes active within a tussock such as, that while one portion is growing another may be senescent. As such, it is a relatively crude means of monitoring growth rates. However, longest leaf method is simple, relatively fast and causes little damage to the tussocks. It is felt that this method provides a reasonable estimate of the relative growth rate of nassella tussock when other, more exact methods are unsuitabl. It is an unsuitable method for comparing tussock sizes in the field.

4.5.2 The Basal Circumference Measurements

It is evident from the results produced from this method that it is unsuitable for monitoring the relative growth rate of nassella tussock. This will be discussed further in a later chapter. There were numerous problems with this method which caused errors or damaged the experimental tussocks. Introducing tussocks through the wire loop and the subsequent pressure around the base dislodged old or rotting leaves. This would give the impression of a decreased rate.. Conversely, tussocks producing flowering tillers were liable to give over-estimates of size because of the enlarged size of these reproductive tillers. Irregularities were caused when debris was either deposited or removed from around and within the tussock bases. It was not possible to ensure that all the debris was removed from the tussocks without damaging the plants. The heavy rains, common in winter, washed soil into the tussock bases or built up the soil around the bases. This resulted in the monitoring of debris depositions and removed more than the actual growth of a tussock. The build up

or removal of soil from around the tussocks also resulted in different levels of the tussocks being measured as the base and thereby introducing further error. This was most noticeable on the steep slopes found in site 3. A further source of error was the moisture content of the soil and tussocks. It was noted that tussock basal circumference increased with an increase in soil moisture content. Therefore, to increase the accuracy of this method it would be necessary to monitor the debris in the tussocks and to maintain a constant soil level around the experimental plants. It would also be necessary to monitor the soil moisture at the time of measuring.

The basal circumference appears to have little value for monitoring relative growth rate. It does, however, appear that basal circumference could be used in conjunction with leaf length in determining the age of tussocks. Although no correlation could be found between leaf length and basal circumference, certain patterns became evident in the field. Tussocks growing in dense shade with moist conditions generally had narrow bases with long, deep green leaves. Tussocks in more exposed, hot, dry areas were usually seen to produce short, pale green leaves and large bases. Therefore, leaf length or basal circumference alone do not always give a true reflection of the age of a tussock.

CHAPTER 5

THE RELATIVE GROWTH RATE UNDER SEMI-CONTROLLED CONDITIONS

The seedlings for this experiment were all germinated in June 1980 during routine germination experiments. After a period of hardening in the laboratory, they were all transplanted on the 7th July 1980, that is, in the middle of winter. The age of all seedlings at the time of transplanting was taken to be one month, although the actual age may have differed by plus or minus one week due to irregular germination. Two sets of five seedlings were processed on the 7th July 1980. These results were taken as the size of the tussocks at the start of the experiment. All calculations of relative growth rate in this experiment were based on the one month old seedlings as being the tussock size at time T_1. Newly germinated seedlings, that is, seedlings only a few days old, were not used because of the difficulties of transplanting and establishing such small tussocks.

5.1 THE RELATIVE GROWTH RATE OF TUSSOCKS GROWN IN 'UNMODIFIED' CONDITIONS IN RHODES ESTATE SOIL

The results have been plotted in histogram form, giving the relative growth rate as the mean, calculated from five tussocks. The criteria that have been used are: change in leaf length; change in the number of leaves; change in the leaf, root and whole tussock mass. The basal circumference could only be measured after 10 months' growth and could, therefore, not be used to monitor the relative growth rate from the seedling stage.

The relative growth rate calculated from longest leaf data

is represented in Figure 5.1 A. The relative growth rate at time T_2, that is after 2 months experimental growth, was large and represents a doubling in leaf length (Table 5.1. This was followed by a large drop in the relative growth rate at T_3 or after 4 months experimental growth. During the next two months the rate increased and showed a large rise after the nine month measure. In absolute terms this means an increase of 9,53 times in nine months. After 11 months the rate remained unchanged but the leaf length actually increased 11,82 times. The 14th month produced a sharp decrease in the relative growth rate.

After 18 months growth in the nursery the relative growth rate showed a very slight increase, from $2,12 \times 10^{-2}$ to $2,329 \times 10^{-2}$ $cm.cm^{-1}day^{-1}$. This represents a total increase in length of 6,9 cm in the last four months of experimentation.

Part B of Figure 5.1 shows the relative growth rate of the same five plants, calculated from the change in the mean number of leaves. The values shown for the eleventh month are an estimation, calculated from the number of tillers. The mean number of leaves per tiller was calculated to be 3,0173. The tillers were not counted in the 14th month because of high tiller production coupled with very short leaves. This made it very difficult to count the tillers. Tillers were again counted in the 18th month when the leaf length had increased and the tussocks were less brittle.

The number of tillers increased from a mean of 4,8 per tussock in the 4th month to 505,6 per tussock in the 18th month. The mean number of leaves increased from 2,4 per tussock at T_1 to 747 in the 10th month. The estimated mean number of leaves per tussock after 18 months was 1 520.

FIGURE 5.1: The relative growth rate of tussocks grown from seed under unmodified conditions in the Nursery of the University of Cape Town.

A. The relative growth rate calculated from leaf length.

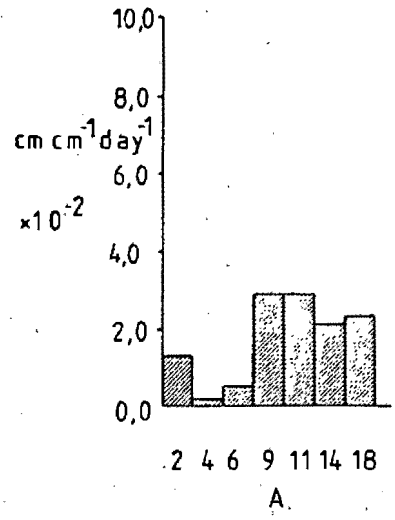
B. The relative growth rate calculated from leaf numbers. The relative growth rate is given as leaves per leaves per time (days).

C. Calculated from leaf mass.

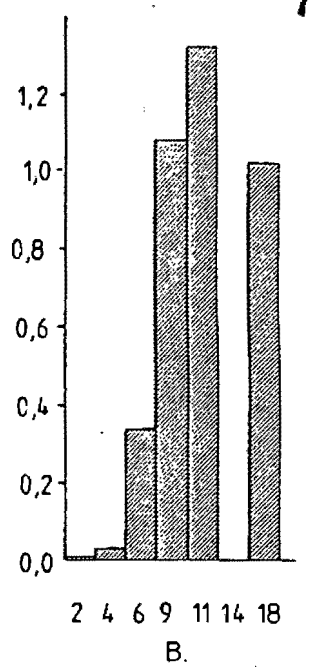
D. Calculated from root mass.

E. Calculated from total biomass.

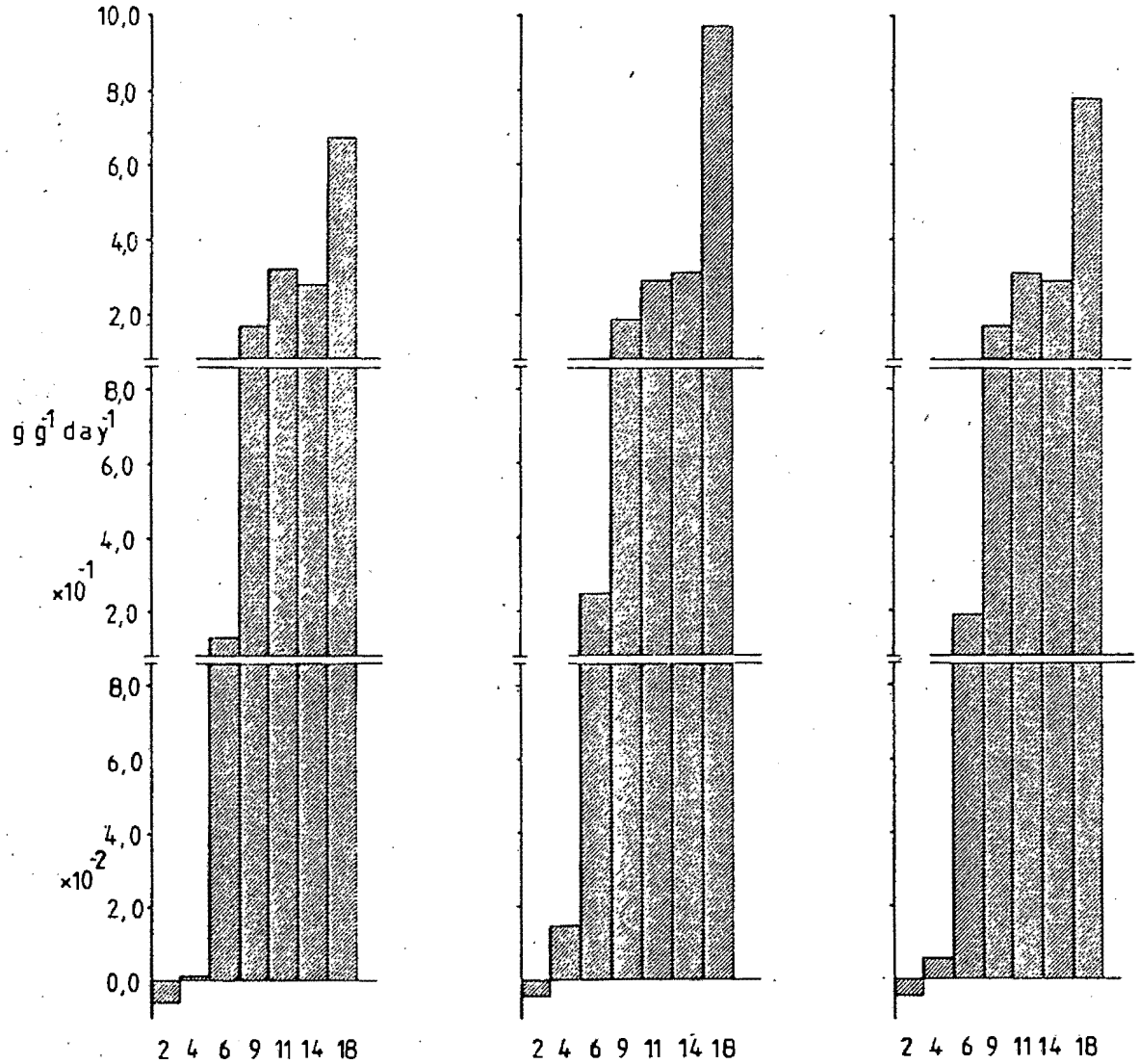
Note: The growth rates were all calculated with the initial value used being that at time zero (T_1), i.e. in all calculations of each section T_1 was constant.


10,0
8,0
cm cm-1 day-1
6,0
×10-2
4,0
2,0
0,0
2 4 6 9 11 14 18

A.


1,2
1,0
0,8
0,6
0,4
0,2
0,0
2 4 6 9 11 14 18

B.


10,0
8,0
6,0
4,0
2,0
8,0
g g-1 day-1
6,0
4,0
×10-1
2,0
8,0
6,0
4,0
×10-2
2,0
0,0
2 4 6 9 11 14 18
2 4 6 9 11 14 18
2 4 6 9 11 14 18
TIME (months) of growth in Nursery

C.

D.

E.

The relative growth rate, using leaf length does not compare very well to that obtained with leaf number. With leaf number (Figure 5.1 B) a steady increase, in the rate, is seen up to the 11th month followed by a decline after 18 months' growth. The rate obtained using leaf length (Figure 5.1 A) shows two declines in the same period. These differences are not unusual as leaf number does not take grazing or damage to leaf ends into account. The two decreased values found with leaf length could be as a result of either grazing or leaf senescence. The first decline is most likely as a result of grazing or physical damage as it is unlikely that 4 month old seedlings would be senescing. The second decrease in the relative growth rate occurred after 14 months. Damage to leaf ends was evident but the cause could not be found. This decrease in leaf length in the 14th month is the time when tillers could not be counted (see above). Both these decreases occurred in spring to early summer, that is, in November (4 months) and September (14 months).

Parts C, D and E of Figure 5.1 show the relative growth rates calculated from leaf, root and biomass respectively. The relative growth rates for leaf and biomass follow the same pattern, increasing to the 11th month followed by a slight decrease in the 14th month. Both recovered to show increased rates in the 18th month. The root mass rates produced a continual increase in rates throughout the experiment. The root mass rates did show a marked slowing down in the 14th month. Although the biomass rates decreased in the 14th month the actual biomass still increased. In the 14th month the biomass was 1 314 times that at T_1. All the relative growth rates based on mass values showed negative values after 2 months. They did, however, show marked increases with values changing from 10^{-3} to 10^{0} $g.g^{-1}day^{-1}$.

One of the aims of this experiment was to check the accuracy

TABLE 5.1: The change in leaf length and total biomass of nassella tussock grown under experimental conditions in Rhodes Estate soil. The experiment was initiated on the 7th July 1980, that is, seedlings were one month old and time equaled zero (or T_1)

Period of time in nursery (months)	Age of Plants (months)	Date		'Unmodified'		70% Shade		Temperate house	
				Mean leaf length (g)	Mean Biomass (g)	Mean leaf length (g)	Mean Biomass (g)	Mean leaf length (g)	Mean Biomass (g)
0	1	07/07/80	$\bar{X}$	1,84	$4,48\times10^{-3}$	1,84	$4,48\times10^{-3}$	1,84	$4,48\times10^{-3}$
			SE	$1,40\times10^{-1}$	$3,78\times10^{-4}$	$1,40\times10^{-1}$	$3,78\times10^{-4}$	$1,40\times10^{-1}$	$3,78\times10^{-4}$
2	3	23/09/80	$\bar{X}$	3,720	$2,90\times10^{-3}$	3,93	$3,740\times10^{-3}$	4,32	$4,420\times10^{-3}$
			SE	$9,023\times10^{-1}$	$5,33\times10^{-4}$	$4,34\times10^{-1}$	$1,585\times10^{-3}$	$7,507\times10^{-1}$	$7,882\times10^{-4}$
4	5	20/11/80	$\bar{X}$	2,350	$8,10\times10^{-3}$	3,55	$6,220\times10^{-3}$	14,59	$1,019\times10^{-1}$
			SE	$3,162\times10^{-1}$	$7,31\times10^{-4}$	$3,037\times10^{-1}$	$1,274\times10^{-3}$	2,82	$3,115\times10^{-2}$
6	7	28/01/81	$\bar{X}$	3,750	$1,785\times10^{-1}$	11,00	$4,400\times10^{-2}$	19,60	$1,90\times10^{-1}$
			SE	1,483	$1,267\times10^{-1}$	1,63	$1,668\times10^{-2}$	2,88	$6,228\times10^{-2}$
9	10	23/04/81	$\bar{X}$	17,55	2,257	12,41	$3,790\times10^{-1}$	32,05	$7,290\times10^{-1}$
			SE	3,22	$5,197\times10^{-1}$	2,99	$1,762\times10^{-1}$	3,93	$1,894\times10^{-1}$
11	12	10/07/81	$\bar{X}$	21,750	5,11	13,70	$2,480\times10^{-1}$	33,55	$9,30\times10^{-1}$
			SE	2,125	1,12*	1,78	$1,397\times10^{-1}$	4,57	$3,877\times10^{-1}$
14	15	29/09/81	$\bar{X}$	19,20	5,88	14,85	$8,480\times10^{-1}$	35,95	3,63
			SE	3,48	1,94	1,64	$1,815\times10^{-1}$	3,23	1,175
18	19	28/01 82	$\bar{X}$	26,10	19,89	36,35	6,38*	60,30	18,27
			SE	3,17	2,74	5,18	3,19	6,86	5,06

of using leaf length for monitoring tussock growth rates. The most striking difference between the rates based on leaf length and mass values is seen after 2 months. The longest leaf results (Figure 5.1 A) produced positive rates of $1,362 \times 10^{-2}$ $cm.cm^{-1}day^{-1}$ while biomass gave $-4,702 \times 10^{-3}$ $g.g^{-1}day$ and leaf mass $-5,371 \times 10^{-3} g.g^{-1}day^{-1}$ (Figure 5.1 C and E). No other major differences except the magnitude of the rates are apparent from these results. It would therefore appear, from this group of tussocks, that leaf length is a fairly true indicator of the growth rate.

5.2 THE RELATIVE GROWTH RATE OF TUSSOCKS GROWN UNDER 70% SHADE IN RHODES ESTATE SOIL

The results for this group of tussocks are shown in Figure 5.2. If these results are compared to those obtained from tussocks grown in 'unmodified' conditions (Figure 5.1) it can be seen that the relative growth rate is lower. This is true for all the criteria used except for leaf length where the rates are similar. The tussocks grown in the shade have a lower biomass (Table 5.1) and leaf production (Figures 5.1 B and 5.2 B). The leaf length, however, remains similar to that in Section 5.1. The relative growth rates calculated from leaf length (Figure 5.2 A) are seen to decrease from the 6th through to the 14th months. This was apparently caused by grazing of the leaf ends as these were severely cut back. The relative growth rates calculated from mass values have a similar pattern to those in Figure 5.1 except that they show lower magnitudes.

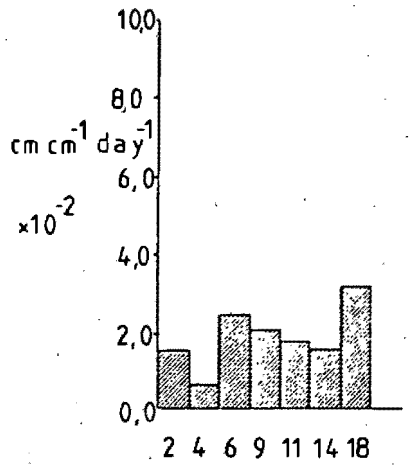
5.3 THE RELATIVE GROWTH RATE OF TUSSOCKS GROWN IN A TEMPERATE GLASS HOUSE

The work carried out in this section is non-qualitative in

FIGURE 5.2: The relative growth rate of tussocks grown from seed under 70% shade in the Nursery of the University of Cape Town.

A. Calculated from leaf length.
B. Calculated from leaf numbers. The growth rate is given as leaves per leaves per time (days).
C. Calculated from leaf mass.
D. Calculated from root mass.
E. Calculated from total biomass.

Note: The growth rates were all calculated with the initial value used being that at time zero (T_1). i.e. in all calculations of each section T_1 was constant.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cm cm-1 day-1
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4,0
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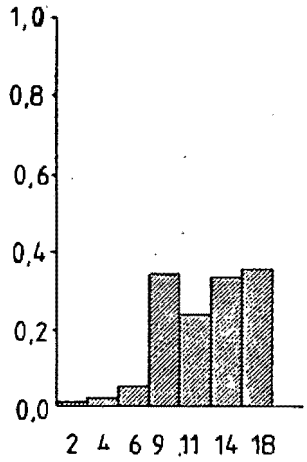
2 4 6 9 11 14 18

A.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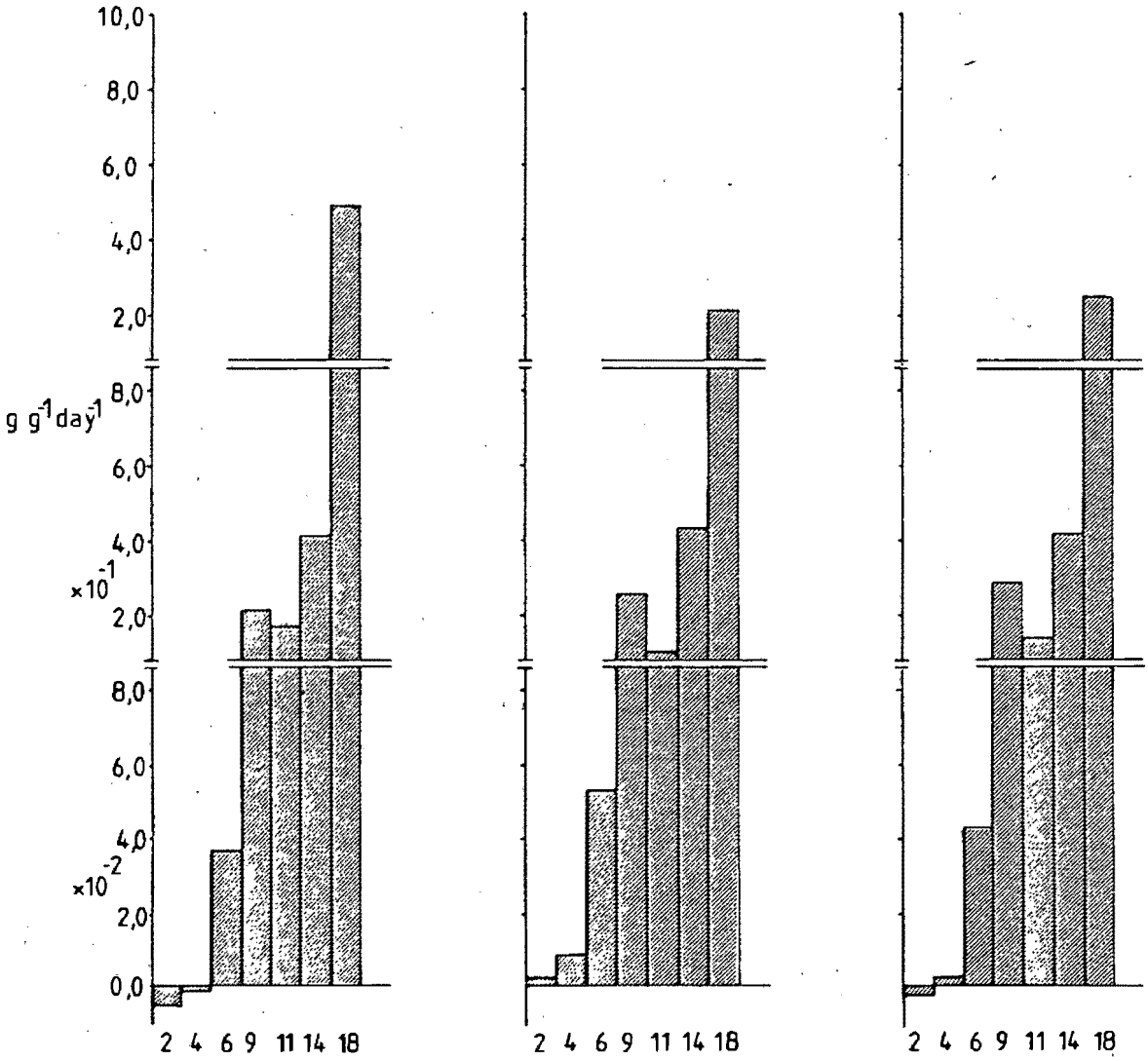
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×10-2
2,0
0,0
2 4 6 9 11 14 18
2 4 6 9 11 14 18
2 4 6 9 11 14 18
TIME (months) of growth in Nursery.

C. D. E.

that the necessary temperature and humidity recordings were not made. This is as a result of inadequate security which prohibited the placing of equipment in the glass-house. The results are included as it is felt that they are representative of the conditions in some of the narrow, humid valleys where nassella tussock is found on Rhodes Estate.

The conditions in the glasshouse consisted of raised temperatures and humity and a slight decrease in light intensity. The tussocks were reliant on artificial watering but could absorb some water from the ground as they were placed in direct contact with the soil surface.

The results of this section are shown in Figure 5.3. The relative growth rate calculated from leaf length (Figure 5.3 A) is seen to be considerably larger than in both the previous sections. The number of leaves (Figure 5.3 B) is intermediate between the other two sections while the rates calculated from plant mass are similar to those of tussocks grown in unmodified conditions.

5.4 DISCUSSION

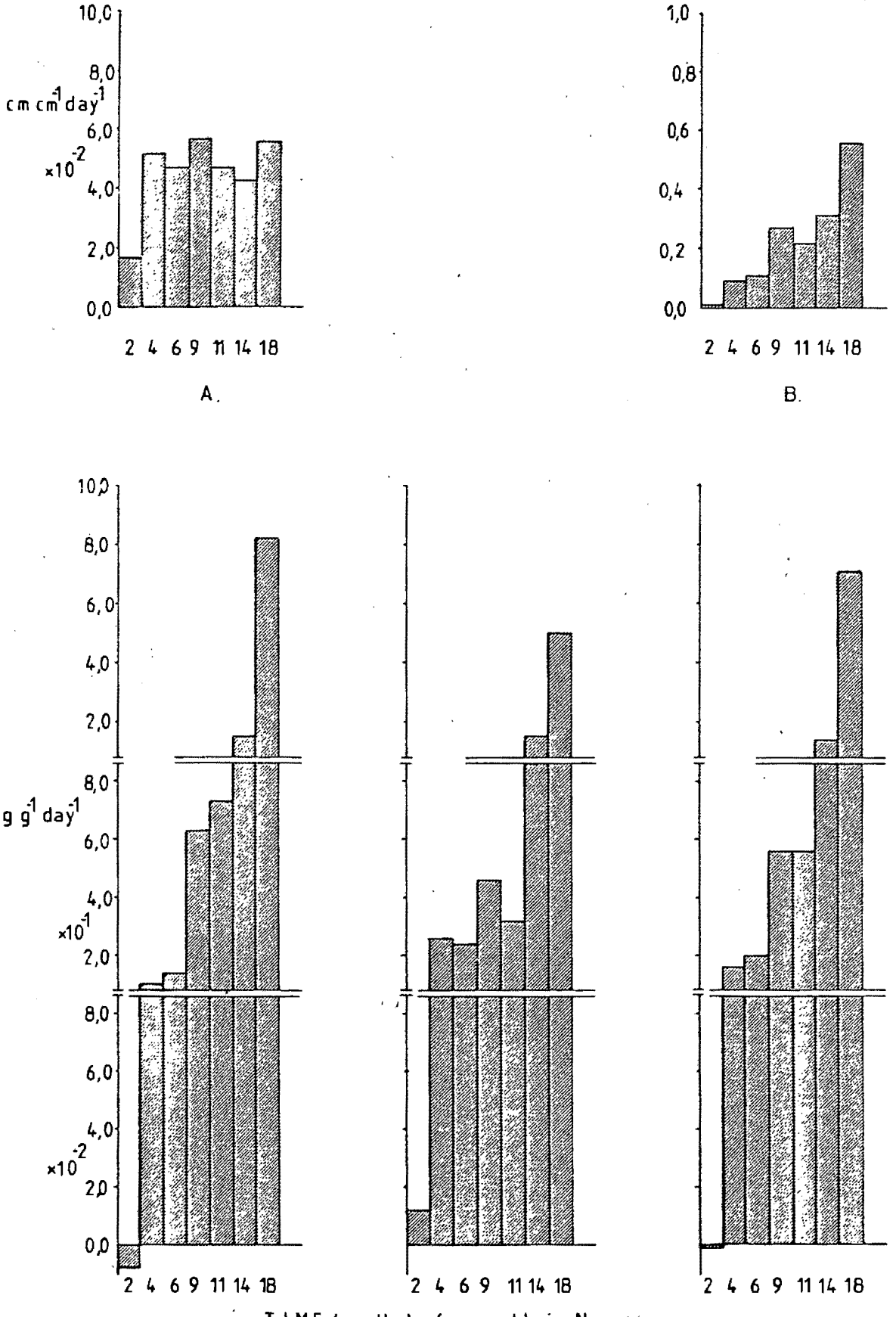
5.4.1 Comparison of Growing Conditions

If the relative growth rate of the three groups is compared using the longest leaf results (A of Figures 5.1, 5.2 and 5.3) it appears that those tussocks growing in the temperate house have the highest growth rate. However, the result from the biomass values show a different pattern. In this case the unmodified environment produced the highest growth rate. (Figs. 5.1, 5.2 and 5.3, Parts E). This difference is partially explained by using the leaf numbers (Parts B). These results show that the unmodified environment produced the highest numbers of leaves, then the temperate house with the shaded tussocks having the lowest rate. Table 5.2, showing the basal circumference from 9 months, takes this further.

FIGURE 5.3: The relative growth rate of tussocks grown from seed under temperate conditions in the Nursery of the University of Cape Town.

A. Calculated from leaf length.
B. Calculated from leaf numbers. The growth rate is given as leaves per leaves per time (days).
C. Calculated from leaf mass.
D. Calculated from root mass.
E. Calculated from total biomass.

Note: The growth rates were all calculated with the initial value used being that at time zero (T_1), i.e. in all calculations of each section T_1 was constant.


10,0
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2 4 6 9 11 14 18
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0,0
2 4 6 9 11 14 18
B.
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8,0
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4,0
2,0
g g-1 day-1
8,0
6,0
4,0
×10-1
2,0
8,0
6,0
4,0
×10-2
2,0
0,0
2 4 6 9 11 14 18
2 4 6 9 11 14 18
2 4 6 9 11 14 18
TIME (months) of growth in Nursery.
C.
D.
E.

The shaded tussocks had the lowest basal circumference throughout, followed by the temperate house tussocks. After 18 months the shade tussocks had a mean circumference of 36,5 mm, the temperate house tussocks, 71,5 mm and the unmodified environment tussocks, 110,5 mm. From Table 5.1 the mean length of the longest leaf is seen to be 36,35 cm for shade, 60,3 cm for temperate house and 26,1 cm for unmodified environment tussocks after 18 months. This shows that under different conditions the tussocks have different patterns of growth. The difference appears to be that shading and a higher humidity with a mild climate produces tussocks with long leaves and narrow tussock bases. Tussocks in the unmodified environment are seen to have short leaves but a larger basal circumference. This phenomenon was also noted in the field where exposed tussocks as at sub-site 1.3 produced shorter leaves and larger bases than tussocks at site 3 which is shaded and moist (see Section 4.5.2).

The relative growth rates calculated from biomass values would be more accurate as the total plant growth rate is being measured. From the biomass values (parts E) it is seen that the unmodified environment tussocks had the highest growth rate with the shaded tussocks being the slowest to grow. However, if Figures 5.1 and 5.3 are compared then parts C show that the growth rate of the leaves is highest in the temperate house tussocks. The root growth is higher in the exposed tussocks. The growth rate of the roots in the shaded tussocks is also lower than the leaf production suggesting that in these less harsh conditions root growth was limited, presumably due to higher moisture contents of the soil.

5.4.2 The Accuracy of Using Leaf Length for Monitoring Growth Rates

The accuracy of the longest leaf for monitoring the relative

TABLE 5.2: The means of tussock basal circumferences, in mm, of tussocks grown under experimental conditions in Rhodes Estate soil. The table shows the date when the tussock bases were first large enough to be measured. The standard error is shown.

Tussock Age	Date		'Unmodified'	70% shade	Temperate house
9 months	23/04/81	$\bar{X}$	42,5 mm	Too	14,0
		SE	4,808	Small	2,57
11 months	10/07/81	$\bar{X}$	64,0	Too	23,75
		SE	9,171	Small	6,24
14 months	29/09/81	$\bar{X}$	67,0	23,5	35,5
		SE	8,638	2,318	5,612
18 months	28/01/82	$\bar{X}$	110,5	36,5	71,5
		SE	7,76	11,74	12,85

growth rate of nassella tussock appears to differ, depending on the conditions under which the tussocks were grown. The relative growth rate calculated from leaf length must be compared with the rate measured by another criterion. The best criteria to use for a comparison would be the number of leaves and biomass growth rates as these are commonly used to monitor growth (Langer, 1972 and Steinke, 1968).

In Figure 5.1, growth under unmodified conditions, the rate of growth, calculated from leaf length declines in the 4th and 14th months. When this is compared with the biomass results it can be seen that only the decrease in rate in the 14th month is shown. The position with the 70% shaded plant is similar except that the decline is from the 9th through to the 14th months (Figure 5.2 A). The corresponding biomass results show a decrease in the 9th month, followed by a marked increase. These similarities between the rates calculated from the leaf length and biomass for the temperate house tussocks are also limited (Figure 5.3). The biomass results show no decrease in the growth rates while the leaf length produced decreases in three months (Figure 5.3 A and E).

Comparing the leaf length rates with those calculated from the number of leaves per tussock produced similar results (Figures 5.1, 5.2 and 5.3, parts A and B). In all the graphs the biomass and leaf number rates follow very similar patterns. The decreases in growth rates recorded with leaf length do not follow any set pattern. In Figure 5.1 A these occur in the 4th and 14th months or in November and September. This could, therefore, be ascribed to a decrease at the onset of the hot summer months. However, the decreases in rates in Figure 5.2 A occur in the 4th, 9th, 11th and 14th month, that is, throughout most of the year. Figure 5.3 A shows decreases in the 6th, 11th and 14th months. This means that the

growth rate recorded in this way decreased, under different conditions during most seasons. It seems probable that these decreases are as a result of leaf damage and not from a reduction in the actual growth.

This places an element of doubt on the validity of the results of the field experiment using the length of the longest leaf to monitor the growth rate. However, the field experiments were based on 50 tussocks per sub-site or 150 per site while the above experiment is based on five tussocks per treatment. Bearing this limitation in mind it is still felt that the field results do indicate the general trends of the relative growth rate. More accurate data would have been obtained if biomass values could have been used.

CHAPTER 6

PHENOLOGY

This experiment was carried out during the 1980 and 1981 flowering seasons, using the same tussocks and sites as were used in Section 4.0. The 1980 season was used as a pilot study. During this season only the time and extent of flowering was monitored. Theextent of flowering was monitored in terms of the number of inflorescences collected from the individual tussocks once the fruits had ripened. In 1981 the flowering process was monitored more intensively with the development of the flowers being noted. The inflorescences were collected, just before the onset of dispersal, placed in plastic bags and air dried in the laboratory. The bags were then sealed and transferred to a cold room at 4°C until counting was done.

6.1 SITE 1

As with the relative growth rates for Site 1, the flowering of the tussocks in this site showed differences between sub-sites 1.3 and 1.1 + 1.2.

6.1.1 Sub-Site 1.1

During the 1980 flowering season the flowering tillers were first seen on the 17th October 1980. At this stage 24 tussocks were found to have started flowering. Nineteen of these had only a few closed flowering tillers. The remaining five tussocks all had more than 20 flowering tillers each, of which about 50% of the inflorescences

had extended from the tiller sheaths. By the 24th November 1980, 60% of the tussocks were flowering. Of this amount, only 4% had fully elongated inflorescences. that is, approximately twice the length of the longest leaf. The rest of the tussocks had inflorescences approximately equal to the length of the longest leaf. This was 5,5 weeks after floral initiation and most of the fruits were well into the milk stage of development (see Section 1.6). At no stage in the floral development had the florets been seen to open for fertilization. According to Campbell (1960) this should have occurred around the fourth week after floral initiation.

In 1981 floral initiation was first seen on the 24th September. No further floral initiation was noted after the 28th October 1981, so the number of plants flowering on this date was taken as 100% (29 tussocks). However, by the 8th October 1981, 96% (28 tussocks) had initiated flowering. This date was taken as time zero in the flowering sequence as it was the date by which most of the tussocks were seen to have started flowering. Table 6.1 shows the events of flowering in sequence giving the event, cumulative percentage and the time lapse from floral initiation. Sixty nine percent of the tussocks had extended inflorescences after three weeks and by the fourth week this had risen to 96%. Only three of these tussocks had florets with green glumes on extension from the sheath. The normal pattern is for the florets to appear from the sheaths with purple glumes and translucent seed coats. The milk stage was well advanced, at 97% after four weeks and 83% of the tussocks had reached the dough stage by the fifth week. The fruits were all taken as ripe on the 12th December 1981 as dispersal was just starting. This makes flowering a nine week process, from the first visible signs of floral initiation to the start of dispersal.

Although only three plants (or 10%) had any florets that

TABLE 6.1: The flowering sequence asat sub-site 1.1 for 1981. The results for each section are cumulative.

Stage in Floral Cycle	Date	% Plants at Given Stage	Days from Time Zero	Weeks from Time Zero
Appearance of floral tillers (initiation)	24/9/81	38%	0	0
	8/10/81	96%	0	0
	28/10/81	100%	0	0
Extension of the inflorescences from the tiller sheaths	28/10/81	69%	20	3
	6/11/81	96%	29	4
	12/11/81	100%	35	5
Extension of the inflorescences above the leaves	12/11/81	83%	35	5
Milk stage	28/10/81	14%	20	3
	6/11/81	97%	29	4
	12/11/81	100%	35	5
Dough stage	12/11/81	83%	35	5

12 plants (or 41%) of dough stage had less than 25% fruits in the dough stage.

3 plants (or 10%) had opening flowers.

3 plants (or 10%) initially had green glumes.

5 plants (or 17%) had purple culm stalks on 12/11/81, i.e. ripe inflorescences.

All taken as ripe and collected on 8/12/81.

opened to expose the anthers and stigmas most of the fruits appeared to be viable.

6.1.2 Sub-Site 1.2

The pattern for the 1980 season in sub-site 1.2 was very similar to that of sub-site 1.1. Inflorescences were first seen on the 17th October 1980, but the quantity was only estimated on the 20th October 1980. At this stage only 12 tussocks were found to have started flowering. By the 24th November 1980, 22 tussocks were flowering. Most of these had inflorescences equal to the length of the longest leaf or were in the milk stage. None of the tussocks had open florets and none of the inflorescences had elongated. The inflorescences were collected in early December 1980 when all the fruits were presumed to be ripe.

In 1981 floral initiation was noted on the 24th September 1981. Table 6.2 shows that extension from the sheath occurred in the fifth week with the milk stage following closely in the sixth week. Eighty-one percent of the tussocks reached the dough stage by the 12th November 1981 or after seven weeks. However, of this 81% (or 21 tussocks), ten had less than 25% of their fruits in the dough stage. This means that the dough stage really occurred in the eighth week, or about the 19th November 1981.

Sub-site 1.2 had three tussocks that had open florets at some stage of the cycle. All the tussocks , except 6, had purple glumes when the inflorescences extended from the sheaths. All the inflorescences were collected on the 8th December 1981, the 11th week after floral initiation.

TABLE 6.2: The flowering sequence as at sub-site 1.2 in 1981. The results in each section are cumulative.,

Stage in Floral Cycle	Date	% Plants at Given Stage	Days from Time Zero	Weeks from Time Zero
Appearance of floral tillers (initiation)	24/9/81	84%	0	0
	16/10/81	92%	0	0
	28/10/81	100%	0	0
Extension of the inflorescences from the tiller sheaths	16/10/81	38%	22	3
	28/10/81	88%	34	5
	6/11/81	100%	43	6
Extension of the inflorescences above the leaves	6/11/81	4%	43	6
	12/11/81	85%	49	7
Milk stage	28/10/81	12%	34	5
	6/11/81	89%	43	6
	12/11/81	93%	49	7
Dough Stage	6/11/81	4%	43	6
	12/11/81	87%	49	7

10 plants (38%) at dough stage on 12/11/81 had less than 25% of fruits in dough stage

3 plants (12%) had opening flowers

6 plants (23%) initially had green glumes

11 plants (42%) had purple culm stalks on 12/11/81, i.e. ripe inflorescences

All taken as ripe and collected on 8/12/81.

6.1.3 Sub-Site 1.3

When the flowering position of this sub-site was first monitored in 1982 the tussocks were already well advanced in flowering. On the 23rd October 1980, 30 tussocks had already started flowering. Of these, 20 had florets that had opened for fertilization. Twenty six of the tussocks had inflorescences extended from the tiller sheaths, with purple glumes while four tussocks had inflorescences just starting to elongate. On the 27th November 1980 34 tussocks were flowering. No tussocks were found with open florets as the cycle was now beyond fertilization. Most of the tussocks had inflorescences that were already elongating and in the dough stage. The inflorescences were collected in early December 1980, well after the fruits were ripe. Collection was delayed due to wet weather which would have resulted in the fruits rotting if collected while they were rain-soaked.

Table 6.3 sets out the sequence of flowering for sub-site 1.3 in 1981. Floral initiation was well advanced at 91% on the 24th September 1981. Extension from the sheaths occurred after three weeks, the milk stage after five weeks and the dough stage after six weeks. Elongation above the leaves started in the fifth week and the fruits were collected as ripe on the 24th November 1981, eight weeks after floral initiation.

In this sub-site only two tussocks had glumes that appeared green which then turned purple. Seventy percent of the tussocks had florets that opened for fertilization. This occurred in mid-October, from the 16th to the 28th October. This is the only sub-site of site 1 where the exposing of the anthers and stigmas was common.

TABLE 6.3: The flowering sequence as seen in sub-site 1.3 in 1981. All results in each section are cumulative.

Stage in Floral Cycle	Date	% Plants at Given Stage	Days from Time Zero	Weeks from Time Zero
Initiation	24/9/81	91%	0	0
Extension of the inflorescences from the tiller sheaths	10/10/81	82%	22	3
	28/10/81	97%	34	5
Extension of the inflorescences above the leaves	28/10/81	82%	34	5
	6/11/81	100%	43	6
Milk stage	28/10/81	85%	34	5
	6/11/81	100%	43	6
Dough Stage	6/11/81	88%	43	6
Collection/Ripe	24/11/81	100%	61	8

2 plants (or 6%) initially had green glumes.

10 plants (29%) had no opening flowers

Flowers opened in mid-October (16/10 - 28/10/81)

6.2 SITES 2 AND 3

Flowering of tussocks in site 2 was monitored only in 1980 and not in 1981. This was caused by the enclosure of the sub-sites which decreased grazing pressures and thereby resulted in the more palatable grasses being able to compete with the nassella tussock. In the 1981 season the plant growth within the enclosures was so dense that it was not possible to single out and mark individual nassella tussocks for study.

In 1980 floral initiation was first noted on the 18th September 1980 with no inflorescences having extended from the tiller sheaths. By 24th October 1980 the tussocks in all three sub-sites were well into the milk stage of development with only a few with floral stalks starting to elongate. In sub-site 2.1 only 18%, sub-site 2 - 22% and in sub-site 2.3 only 9% of the tussocks had stalks elongating. Both sub-sites 2.1 and 2.2 had 58% and 42% respectively, of their tussocks with florets that were opening for fertilization. In sub-site 2.3 only 18% of the tussocks had open florets.

In site 3 flowering was very limited. In 1980 only 40% of the tussocks in this site produced flowers with only a few inflorescences, usually less than 20 per tussock. No tussocks had florets opening for fertilization and green glumes were fairly common. In 1981 only sub-site 3.1 produced flowers and then only in November, about a one month delay from sites 1 and 2. By the 12th November 1981 extension of the inflorescences beyond the sheaths had just started. Seventy percent of the tussocks produced florets with green glumes. No open florets were noted and the fruits were harvested in mid January 1982.

6.3 REPRODUCTIVE POTENTIAL

6.3.1 Inflorescence Production

In Table 6.4 the mean number and the highest and lowest number of inflorescences produced per tussock are shown. If the results for the 1981 season are taken it can be seen that the mean number of inflorescences per tussock is very similar for all the four sub-sites sampled. The highest number of inflorescences per tussock in 1981 was 151 in sub-site 1.3 and the lowest of 3 in sub-site 3.1.

During 1980 the results are not as reliable. The figures shown in Table 6.4 for sub-sites 1.1 and 1.2 represent the inflorescences of 9 and 8 plants respectively. This is because the remainder of the samples were accidently destroyed before counting. Sub-site 1.3 shows a higher floral production in 1980 than in 1981, by about 20 inflorescences per tussock more. Sub-site 2.3 which has been used as a representative of site 2 shows a significantly higher floral production than any of the other sites. The mean number of inflorescences per tussock is 157, with a maximum of 787 from one tussock.

For these results to be of any value one needs to look at the age or size distribution of the tussocks within the sites. This would give a pattern of floral production in relation to size and age of the tussocks within a site (Section 6.3.3).

6.3.2 Fruit Production

The counting of fruits is an arduous and time consuming task. The fruits have to be removed manually from the inflorescences and then sorted from the broken stalks and

TABLE 6.4: The floral production of some of the experimental sub-sites on Rhodes Estate. The table shows the mean number of inflorescences produced per tussock in five sub-sites and compares results from two seasons. The table also shows the highest and lowest number of inflorescences recorded on tussocks.

Locality		1980	1981
Site 1.1	Sum	20	1 078
	N	9	28
	$\bar{X}$	2,2	38,2
	SE	0,2	5,1
	High	3	101
	Low	1	6
Site 1.2	Sum	21	804
	N	8	23
	$\bar{X}$	2,6	34,9
	SE	0,375	4,4
	High	4	77
	Low	1	5
Site 1.3	Sum	1 716	1 325
	N	29	34
	$\bar{X}$	59,1	38,9
	SE	8,3	4,9
	High	164	151
	Low	10	6
Site 2.3	Sum	3 313	
	N	21	
	$\bar{X}$	157,7	
	SE	38,1	
	High	787	
	Low	24	
Site 3.1	Sum	756	1 232
	N	19	32
	$\bar{X}$	39	38,5
	SE	6,4	5,2
	High	113	118
	Low	2	3

glumes. The complete process of separating, cleaning and then counting the fruits of a tussock with about 30 inflorescences will take more than 1,5 hours. To give an accurate account of the number of fruits produced would not have been much more enlightening than the number of inflorescences per tussock. Healy (1945) gave the range of fruit production per inflorescence as between 20 and 110, with most having between 55 and 70.

In this study the fruit production of 34 tussocks was calculated. The lowest mean number of fruits per inflorescence was 15,6, in sub-site 1.2. The highest found was 88 fruits per inflorescence, in sub-site 1.3. Sub-site 1.3 was used as a representative of Rhodes Estate and the fruits of 16 of its 34 tussocks were counted. The mean number of fruits per inflorescence was 65,42. This figure corresponds well with the average found by Healy (1945). If this figure is used to estimate the fruit production per tussock from the data in Section 6.3.1, it can be seen that the mean fruit production per tussock is fairly low. The highest number of inflorescences produced on one tussock was 787 in sub-site 2.3. This gives a fruit production of 51 485 fruits per tussock. However, this was an abnormally high figure for the Estate and all the other sites have means of about 38 inflorescences per tussock (Table 6.4). This gives a fruit production of 2 485 fruits per tussock. It is likely then that this figure would represent an approximate mean for Rhodes Estate while a few plants will produce many more.

Comparisons with other grasses are difficult because most seed estimates are given as the number of seeds produced per unit area or as kilograms seeds per hectare. Jones (1968) working on the seed production in secondary succession in the South African highveld found that seed output varied, depending on the position of the seral stage of the grass. Aristida congesta Roem. + Schult. a primary

grass produced 1 110 seeds per plant and Eragrostis curvula Nees produced 6 050 per plant. The mean value obtained for primary grass seed production was 6 200. Secondary grasses have a lower seed output at 272 seeds per plant while sub-climax species produced a mean of 27 seeds per plant (Jones, 1968). These figures, although not for weeds, show that the nassella tussock on Rhodes Estate has a relatively high fruit production. This is even though the population on Rhodes Estate appears to be immature. The fruit production of 51 485 at site 2.3 and Well's (1974) estimate of 100 000 fruits per tussock are seen to be very high.

6.3.3 Site Age Structures

For both floral and fruit production to be of value it is necessary to look at the age or size distribution of the tussocks within the experimental sites.

Figure 6.1 shows the size distribution of tussocks in site 1. The leaves were measured and the tussocks divided into 5,0 cm size classes. When Table 6.5 is used in conjunction with Figure 6.1 it is seen that the 95 plants per square metre in sub-site 1.1 are found mostly in the size classes of less than 25 cm. The pattern for sub-sites 1.2 and 1.3 is very similar with all the sites showing a large proportion of short leaved tussocks. Basal diameter was used as a second criterion and this follows the same pattern as the length of the longest leaf. This shows that these are young communities and are unlikely to have reached their flowering maturity. Figure 6.2 shows the same results for site 2. In this site, the number of tussocks per square metre is lower than in site 1, from 7,0 to 14,5 plants per square metre (Table 6.5). However, the majority of the tussocks are found in the range of 20 to 45 cm, calculated from the length

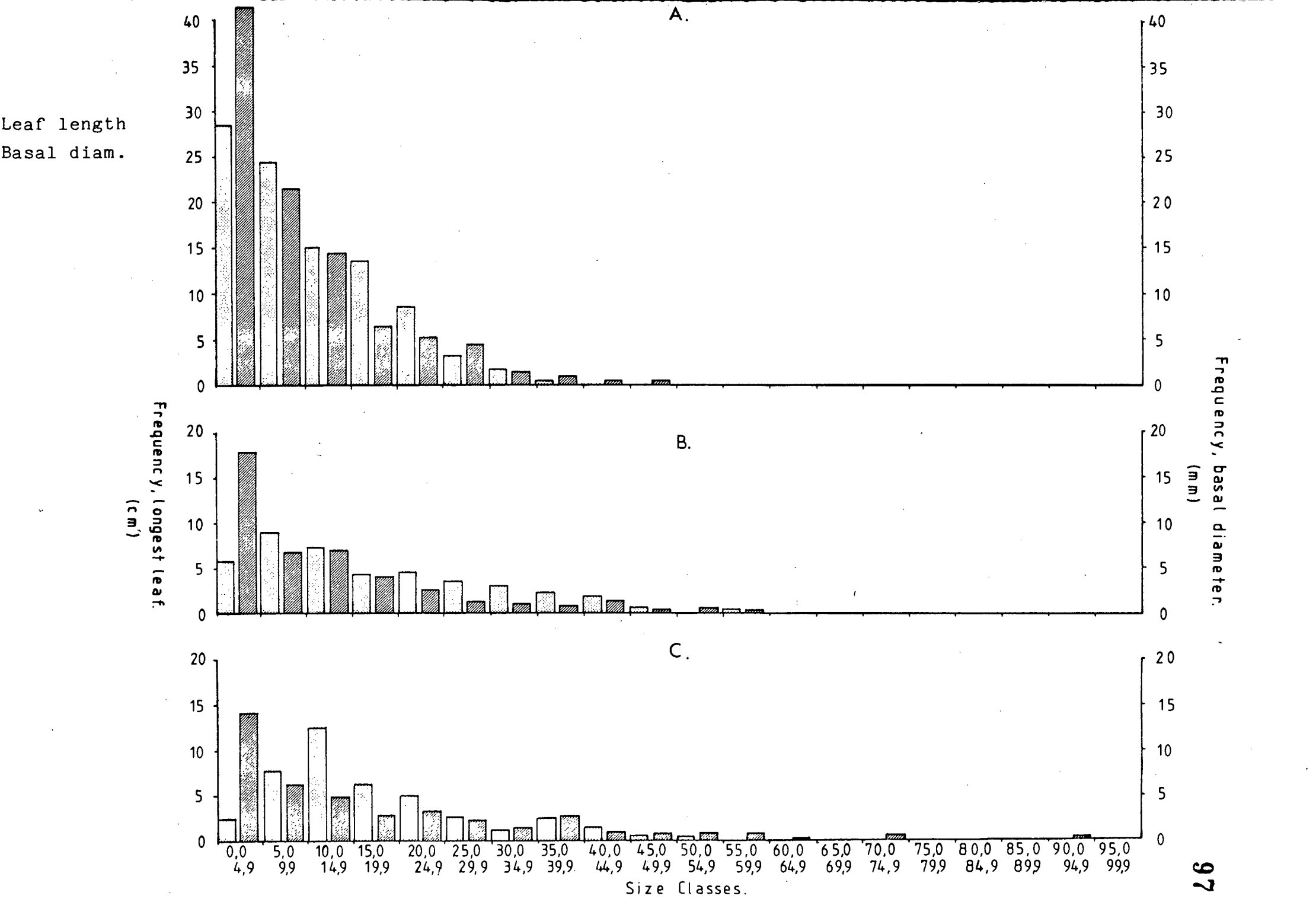
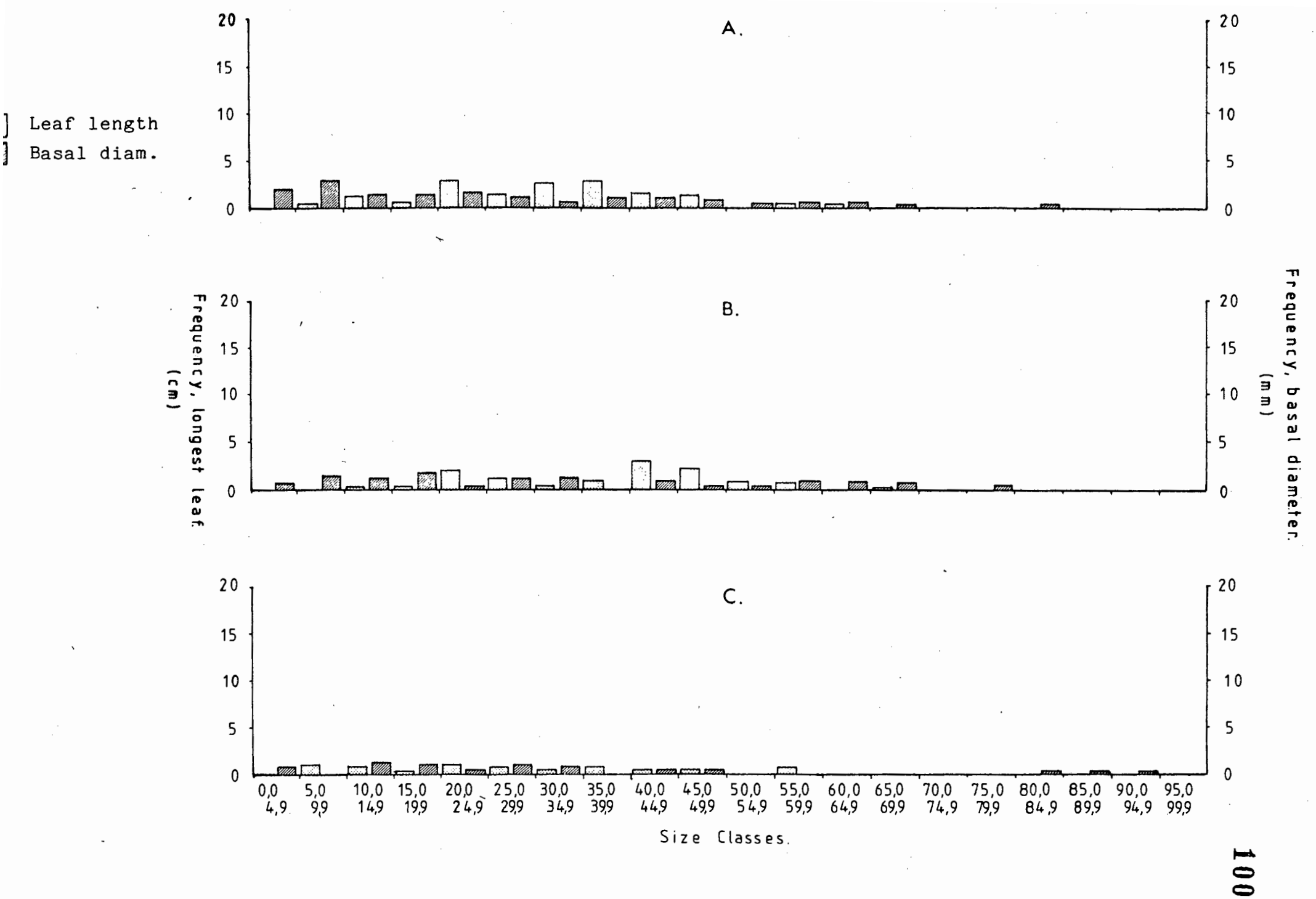

Leaf length
Basal diam.
A.
B.
C.
Frequency, longest leaf. (cm)
Frequency, basal diameter. (mm)
0,0 4,9
5,0 9,9
10,0 14,9
15,0 19,9
20,0 24,9
25,0 29,9
30,0 34,9
35,0 39,9
40,0 44,9
45,0 49,9
50,0 54,9
55,0 59,9
60,0 64,9
65,0 69,9
70,0 74,9
75,0 79,9
80,0 84,9
85,0 89,9
90,0 94,9
95,0 99,9
Size Classes.

TABLE 6.5: The number of tussocks per square metre as found in the three sites. The figures are the means of 4 quadrats of 1 m² each

Sub-Site	Site		
	1	2	3
.1	95	14,5	16,75
.2	39,5	12,5	5,5
.3	40	7,0	2,75


Leaf length
Basal diam.
A.
B.
C.
Frequency, longest leaf (cm)
Frequency, basal diameter (mm)
0
5
10
15
20
0,0 4,9
5,0 9,9
10,0 14,9
15,0 19,9
20,0 24,9
25,0 29,9
30,0 34,9
35,0 39,9
40,0 44,9
45,0 49,9
50,0 54,9
55,0 59,9
60,0 64,9
65,0 69,9
70,0 74,9
75,0 79,9
80,0 84,9
85,0 89,9
90,0 94,9
95,0 99,9
Size Classes.

of the longest leaf. This shows a more mature community having fewer young tussocks. This corresponds to its high floral production as shown in Section 6.3.1.

The size classes for site 3 are shown in Figure 6.3. A noticeable difference is seen in that sub-site 3.1 has more tussocks per square metre (16,75) than either sub-sites 3.2 or 3.3 (5,5 and 2,75 respectively) (Table 6.5 and Figure 6.3). The number of tussocks per square metre is, on average, much lower than that of sites 1 and 2. There is no distinguishable peak of size class in site 3, with tussock size classes ranging from less than 5,0 cm to less than 70 cm (longest leaf). This site appears to be more mature than sites 1 and 2 and would thus be expected to have a higher floral production. Section 6.3.1 showed that this was not the case and the floral production of this site was the same as that of site 1.0. This is probably due to the dense shading of the site which reduces flowering and also the relative growth rate (Section 4.3).

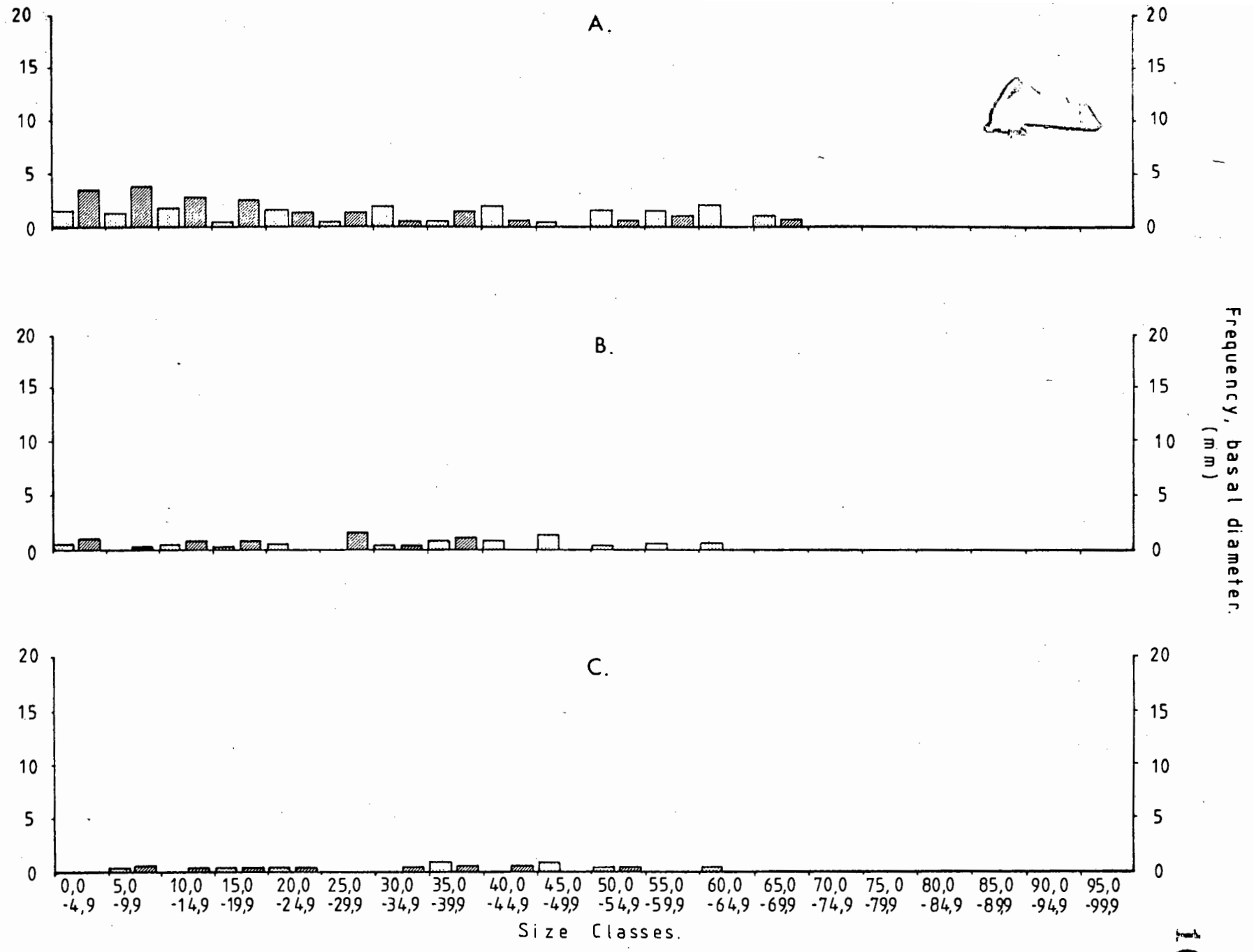
6.4 VARIATIONS IN FRUIT SHAPE AND SIZE

It was noted that fruit shape varied considerably within and between different samples. The major variation was found in fruit size and shape. If one excludes non-viable fruits which can be seen as small, pale yellow to white fruits that are readily squashed between the fingers, then there are two varieties of fruit shape.

Fruits from site 1.3 were separated into the two classes and then measured with the aid of a microscope. Figure 6.4 shows the results of this experiment. One hundred fruits of each class were measured and then plotted as a scatter diagram as fruit length versus breadth. It can be seen from Figure 6.4 that the two classes are clearly

FIGURE 6.3: The distribution of size classes of tussocks at site 3. The size classes are given for both leaf length (cm) and basal diameter (mm). Section A is for sub-site 3.1, B for 3.2 and C for 3.3.

Leaf length
Basal diam.



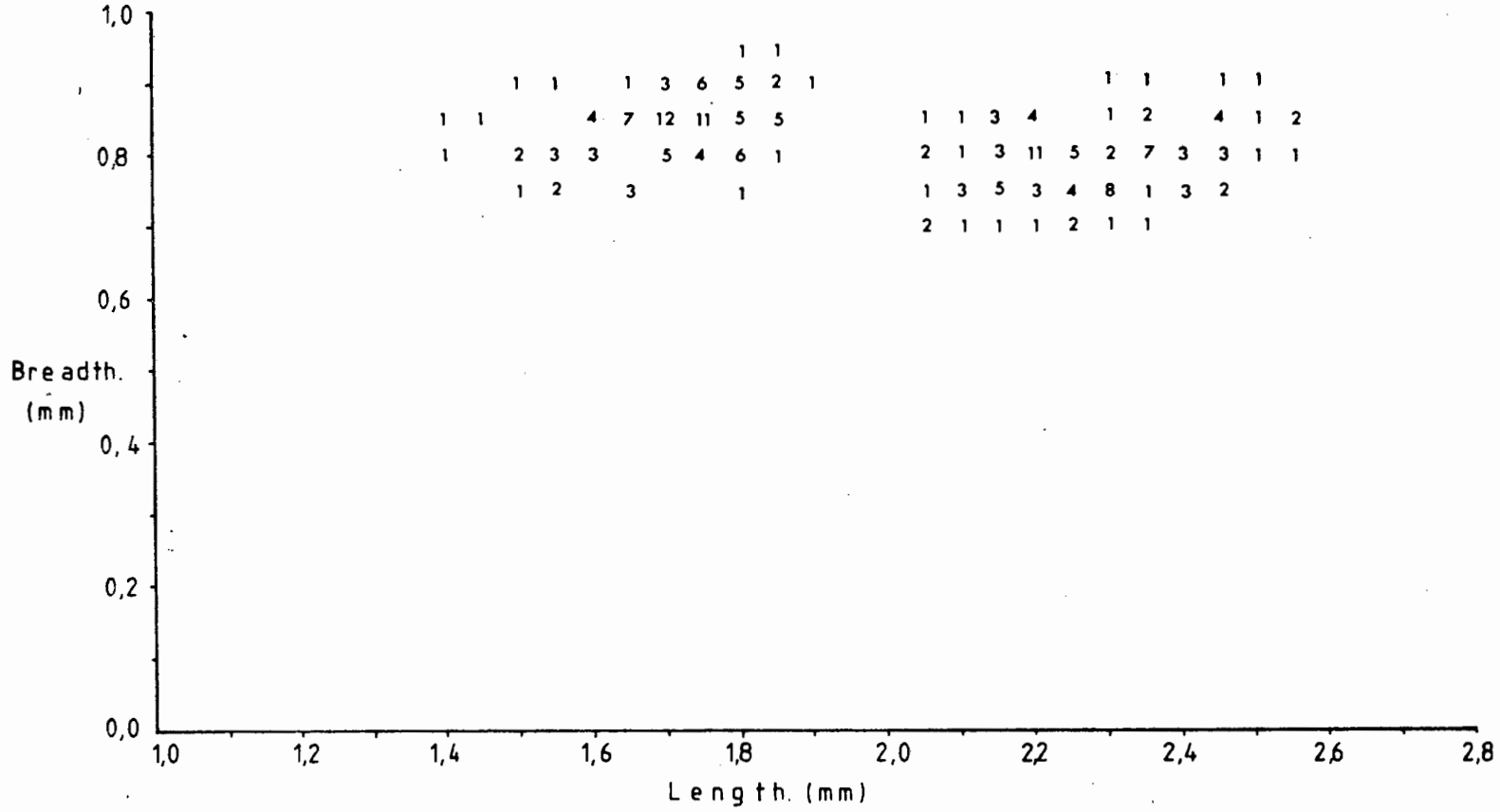


FIGURE 6.4: A scatter diagram showing the length and breadth of two hundred sorted fruits from sub-site 1.3. The figures represent the number of fruits in each category.

different. The first class appears as short fat fruits, less than 1,95 mm in length. The second class appears as long thin fruits, more than 2,00 mm in length. Although the fruits have been classified as short, fat and long, thin, the breadth of the fruits appears to be the same in both classes. However, if the same data are plotted as a ratio, that is, fruit length divided by fruit breadth, then a very clear difference between the classes is seen (Figure 6.5).

These differences in fruit shape are not as marked in all the samples of fruits collected. Random samples of fifty fruits each were taken from each field site and then measured. The results are shown in Figure 6.6. Figure 6.6 A shows the mean fruit length in mm, 6.6 B the mean fruit breadth, in mm, and 6.6 C the ratio of length to breadth.

It can be seen that in site 1 only sub-site 1.3 has long fruits while in sub-sites 1.1 and 1.2 the fruit length is significantly shorter (Figure 6.6 A). However, the position is reversed when one looks at fruit breadth (Figure 6.6 B) and sees that in sub-sites 1.1 and 1.2 the fruits are significantly fatter than in sub-site 1.3. In site 2 there is no significant difference between the sub-sites with all producing long, moderately fat fruits. Sub-site 3.1 has short, fat fruits that are intermediate between sites 1 and 2.

The length/breadth ratios (Figure 6.6 C) can be used to determine the difference in fruit shape in plants growing in close proximity to each other. Sub-sites 1.1, 1.2 and 3.1 are the sites that experience the most shading from trees. Sub-site 1.3 is found on an exposed slope and is shaded only marginally by the surrounding stone pine trees. All the sub-sites of site 2 are exposed and

Figure 6.4

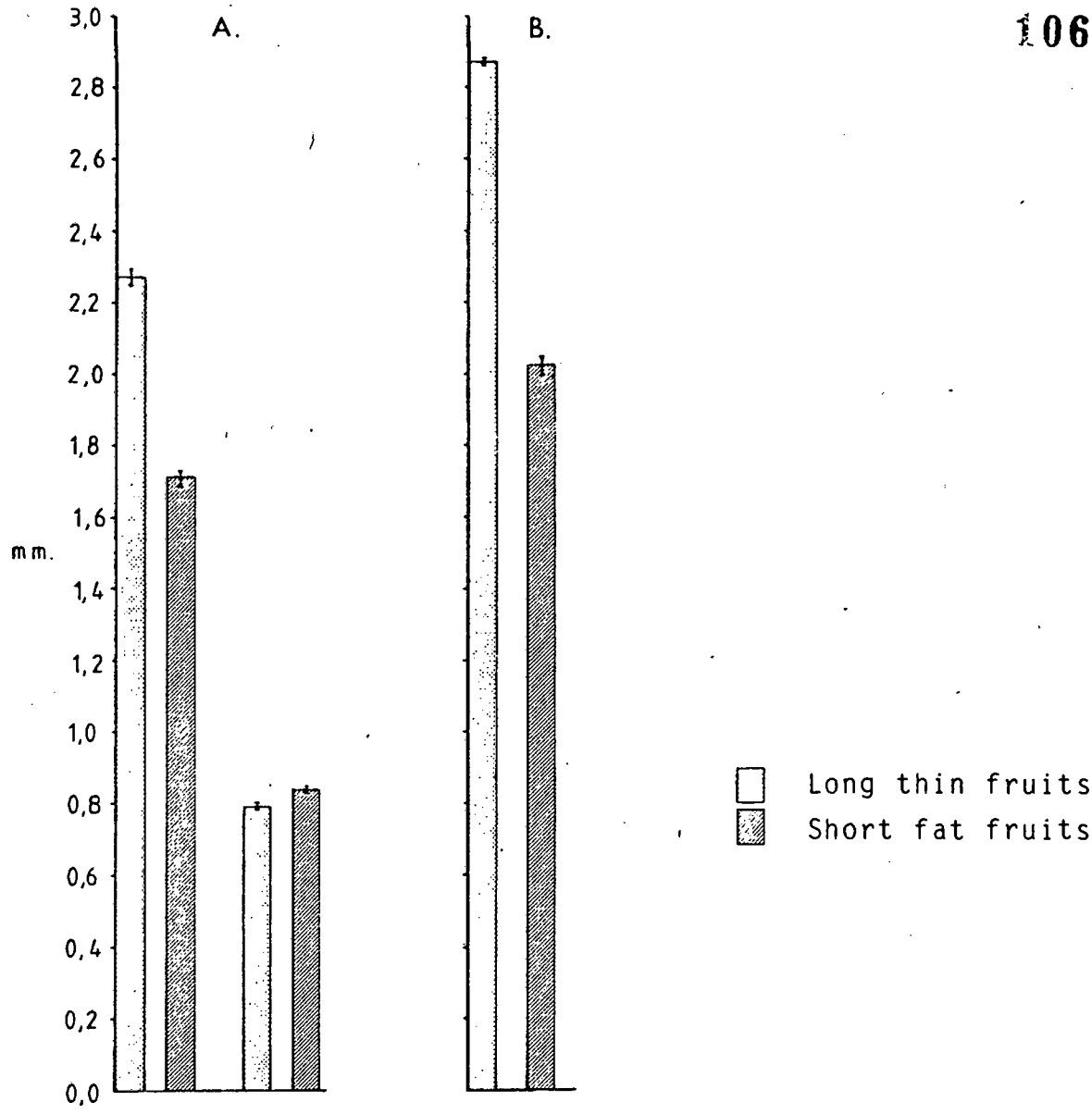


FIGURE 6.5: Part A shows the same results as Figure 6.4. In Figure 6.4 the breadth of the fruits appeared equal. Here it can be seen that the breadths of the two classes of fruits are significantly different at the 95% confidence limits.

Part B shows the results expressed as the ratio of length over breadth.

the inflorescences experience only self shading. It would therefore appear that fruit shape could be associated with the degree of exposure to direct sunlight or shading.

In Section 6.3 mention was made of whether florets exposed their anthers and stigmas during fertilization or not. If this information is coupled to length/breadth ratios (Table 6.6), we find two extreme situations. Sub-site 1.3, with a length/breadth ratio of 2,446 had 70% of its tussocks with florets opening for fertilization and sub-site 3.1, with a ratio of 1,985, had no open florets. Both sub-sites 1.1 and 1.2 with ratios of less than 2,0 had 10 and 12% respectively, of their tussocks with open florets. Sub-sites 2.1 and 2.2, with ratios of more than 2,00 had 58 and 42% respectively of their tussocks with open florets. Only sub-site 2.3 had a ratio of more than 2,0 and only 18% of the tussocks with open florets. This then suggests that fruit shape is associated either with the degree of shading or with the occurrence of open florets.

When the fruits of different tussocks were examined in the field the dried remains of the anthers could often be seen still attached to the lemma (Plate 9.1 C). The anther remains were easily dislodged so that this phenomenon was seldom noted in material brought into the laboratory. However, the occurrence of the anther remains was only noted in tussocks growing in the sun and then only on the long, thin fruits. At no stage were stigmas seen to be exserted without the appearance of the anthers. This points to a dual strategy in the fruit production of nassella tussock:

1. shaded tussocks, or inflorescences, result in self fertilization which produces short, fat fruits;

2. tussocks or inflorescences growing in strong sunlight have florets that open for cross fertilization and produce long, thin fruits.

TABLE 6.6: The percentage of tussocks per sub-site with open florets and the ratio of fruit length versus fruit breadth.

Site	Year	% plants with open florets	Length/breadth ratio
1.1	1981	10	1,914
1.2	1981	12	1,9
1.3	1981	70	2,446
2.1	1980	58	2,214
2.2	1980	42	2,210
2.3	1980	18	2,235
3.1	1981	0	1,985

At no stage were all the florets on any inflorescences seen to be opening. The occurrence of open florets even in sub-site 1.3 was always found to be less than 100% and to vary from one inflorescence to another.

6.5 DISCUSSION

The process of flowering in nassella tussock on Rhodes Estate can be classified into the following stages and times:

1. in Floral initiation from the end of September through to the end of October. This varies from site to site and season to season.

2. extension of inflorescences from the tillers at 3 to 4 weeks after initiation.

3. extension of inflorescences above the leaves at 5 to 6 weeks after initiation.

4. milk stage is found at 5 to 6 weeks after initiation.

5. dough stage at 7 weeks after initiation.

6. fruits are ripe at approximately 8 weeks after floral initiation.

Open florets were seen at approximately 4 weeks into the floral cycle.

The tussocks were considered to be at any given stage in the floral cycle when approximately 75% of their inflorescences had reached that stage. A site was taken to be at any given stage in the cycle when approximately 80% of its tussocks had reached that stage in the cycle.

The pattern shown here for Rhodes Estate differs only slightly from that given by Campbell (1965) for the Central Tablelands, New South Wales. The most significant differences are the colour of the glumes on first appearance and the extent of anther and stigma emergence. Campbell (1965) found that the glumes and outer coats of the spikelets appear green and translucent as they extend from the leaf sheath. On Rhodes Estate this occurred only occasionally. In most cases the glumes appeared purple and the lemma and palea translucent. Campbell (1965) then discussed the emergence of the anthers and stigmas from the florets suggesting that it was a common occurrence found in all the tussocks studied. This, however, is not the case with the Rhodes Estate population. In this population the extension of anthers and stigmas appears to be regulated by the extent of shading. At no time was anther and stigma extension found to dominate a tussock or population.

The floral production on Rhodes Estate is lower than that found by Healy (1945). On Rhodes Estate the highest number of inflorescences per tussock was 787 while Healy (1945) readily found as many as 1 000 and more inflorescences per tussock. However, Healy (1945) found that the floral production in immature stands could be as low as 3 inflorescences per tussock. It was not uncommon on Rhodes Estate to find tussocks with only one inflorescence.

Estimates of floral production in nassella tussock have been carried out by Healy (1945) and Campbell (1965) to determine its invasive capabilities. These workers have been dealing with nassella tussock in relation to agriculture and the infestations do not appear to have the chequered control history of Rhodes Estate. This makes a direct comparison of results difficult. However, Healy's (1945) figures for an immature infestation are similar to the

results obtained in this case. These correspond to results showing that most of the study sites consist of immature tussocks. The one site, site 2, that appeared, by comparison to the other sites, to be mature would actually be immature when comparing it with Healy's (1945) results. It is impossible to give an actual age for any of the sites as the clearing programme is random and no records have been kept as to when the areas were cleared. From Table 6.5 it can be calculated that the mean number of tussocks per square metre is 26. From Table 6.4 the mean number of inflorescences per tussock can be calculated at 42. In Section 6.3.2 the mean number of fruits per inflorescence is given as 65. This can then be calculated to give an estimated fruit production of more than 70 000 fruits per square metre. However, the whole Estate is not covered to this extent so the actual figure will be much lower. This does show that although the infestation is being cleared and is mainly immature, the fruit production is still high.

CHAPTER 7

GERMINATION

Some of the physiological aspects of the germination of nassella tussock fruits are dealt with by Joubert (1980). In his account he dealt with light, temperature and chemical aspects of germination. The studies to be discussed in this chapter were designed to investigate the germination of nassella tussock fruits under field conditions. The use of chemicals was excluded and only those parameters that could have a direct influence on fruits in the field were investigated.

Attempting to analyse the germination of nassella tussock as it would occur under field conditions imposed certain restrictions on the experiments. The most noted of these was the effect of not using any surface sterilization of fruit stocks to prevent fungal activity. Surface sterilization of the fruits and naked caryopses was not undertaken as it was felt that microbial action could play a role in the germination. This resulted in varying degrees of fungal infestation in the germination trials which in a few cases resulted in the early termination of the experiment.

Fungal activity was generally noted after about 21 days of fruit germination. This period fluctuated between experiments. Most experiments could, however, be run successfully for 21 days and this period was found to be suitable for the germination of nassella tussock fruits. Twenty-one days was therefore chosen as an arbitrary termination date for most experiments. When working with naked caryopses it was found that fungal activity was predominant after 10 to 15 days germination. Fungal activity on naked caryopses was noted to be more severe

than on the fruits. The fungus responsible was not identified.

7.1 THE RATE AND PERCENTAGE GERMINATION

Initial experiments were aimed at determining the rate and percentage germination of intact, untreated nassella tussock fruits, that is, with the lemma and palea still attached. The first results obtained have not been included as the final percentage germination was less than 5% after 3 weeks. However, in subsequent experiments, using the same fruit stock and experimental conditions, the percentage germination increased, possibly due to some ripening process. In Figure 7.1 this can be seen to have reached 10% after 21 days. These experiments were carried out on fruits that had been collected in 1979 by another worker and the history of collection and storage was scant.

Using fruits collected in 1980, from sub-site 2.3, and then stored at 4°C until used, a much higher percentage germination was obtained. The rate of germination was higher (Figure 7.1), about 40% in 10 days compared to approximately 5% in the same period with the 1979 fruits. The level of germination of the 1980 fruits after 21 days was 60%, which was felt to be relatively low for a plant reputed to be an aggressive invader. However, these results are similar to those found by Healy (1945) and Joubert (1980). Healy found that nassella tussock seldom reached more than 50% germination after 40 days and long periods, in the order of 800 days were required for germination in the order of 80%. Joubert (1980) found that the germination of intact fruits was low, but could be increased by removing the lemma and palea.

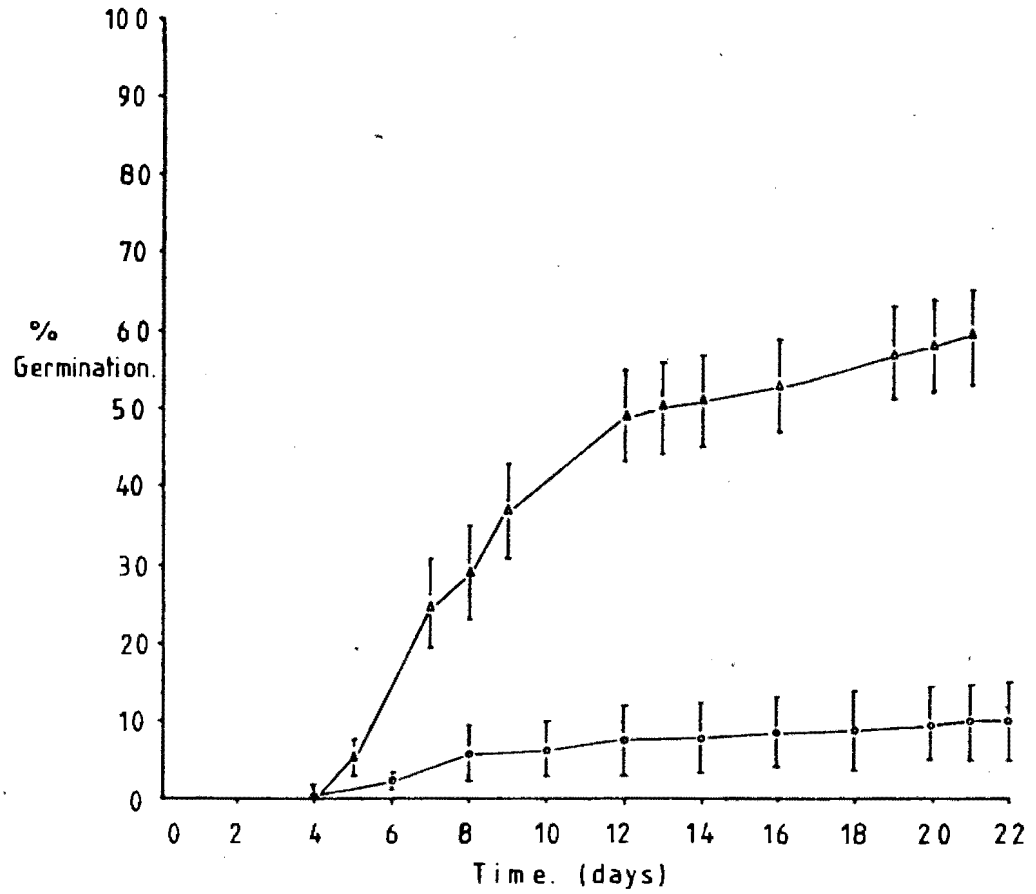


FIGURE 7.1: The rate of germination of untreated nassella tussock fruits. The margins shown are standard error, not confidence limits.

- Initial level of germination using fruits of unknown history.

- Fruits from sub-site 2.3 (1980).

7.2 THE REMOVAL OF THE LEMMA AND PALEA

The lemma and palea were removed from fruits and the naked caryopses were used for germination experiments. Naked caryopses from sub-site 2.3 were used, with intact, untreated fruits serving as a control. The results are shown in Figure 7.2. The rate of germination of the naked caryopses (circular dots) is high with 65% germination being achieved in 8 days. Unfortunately the caryopses were very susceptible to fungal attack and the experiment had to be terminated after only 11 days. However, a comparison of initial rates is possible. The intact, untreated fruits produced a much lower germination rate and had only attained 36% after 8 days. From Figure 7.2 it is clear that had the germination of the naked caryopses been continued for longer, the final level of germination would have probably been in the same order as that of the fruits. It would appear, therefore, that although the removal of the lemma and palea increased initial rates, it had little effect on the end result, i.e. the percentage germination.

The experiment was repeated, using fruits and naked caryopses from tussocks growing about 100 metres south east of sub-site 1.1. The conditions under which these tussocks were growing were very similar to those found at sub-site 1.1. The intact fruits from these tussocks were found to be slow germinators with a very low percentage germination (Figure 7.3). Intact, untreated fruits gave 2% germination after 21 days. This level of germination was increased many-fold by the removal of the lemma and palea (Figure 7.3). This resulted in a higher rate of germination and 50% germination after 21 days.

The aim of this experiment was to determine whether the Western Cape population of nassella tussock differed from the Eastern Cape population, in their response to the removal

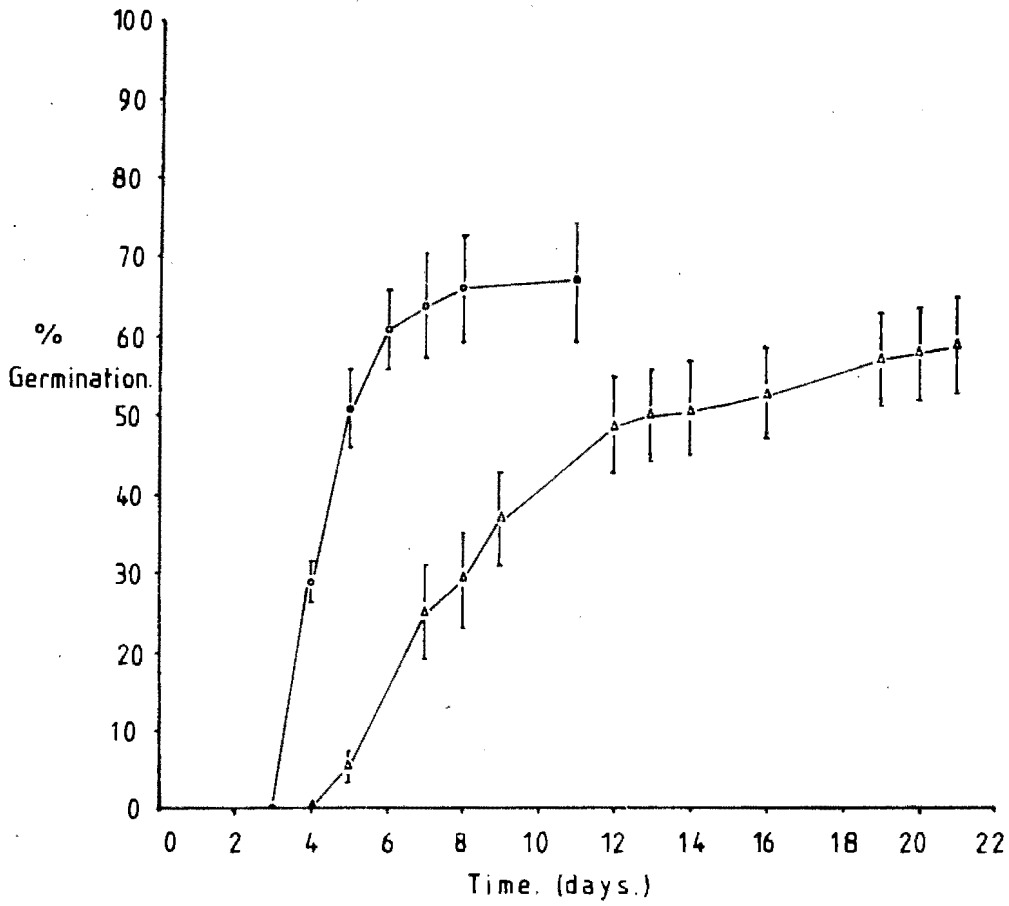


FIGURE 7.2: The effect of the removal of the lemma and palea on the germination of nassella tussock. Intact fruits were used as a a control. The standard error is shown.

▲ Control, untreated fruits from sub-site 2.3.

● Caryopses (fruits minus lemmas and paleas) from sub-site 2.3.

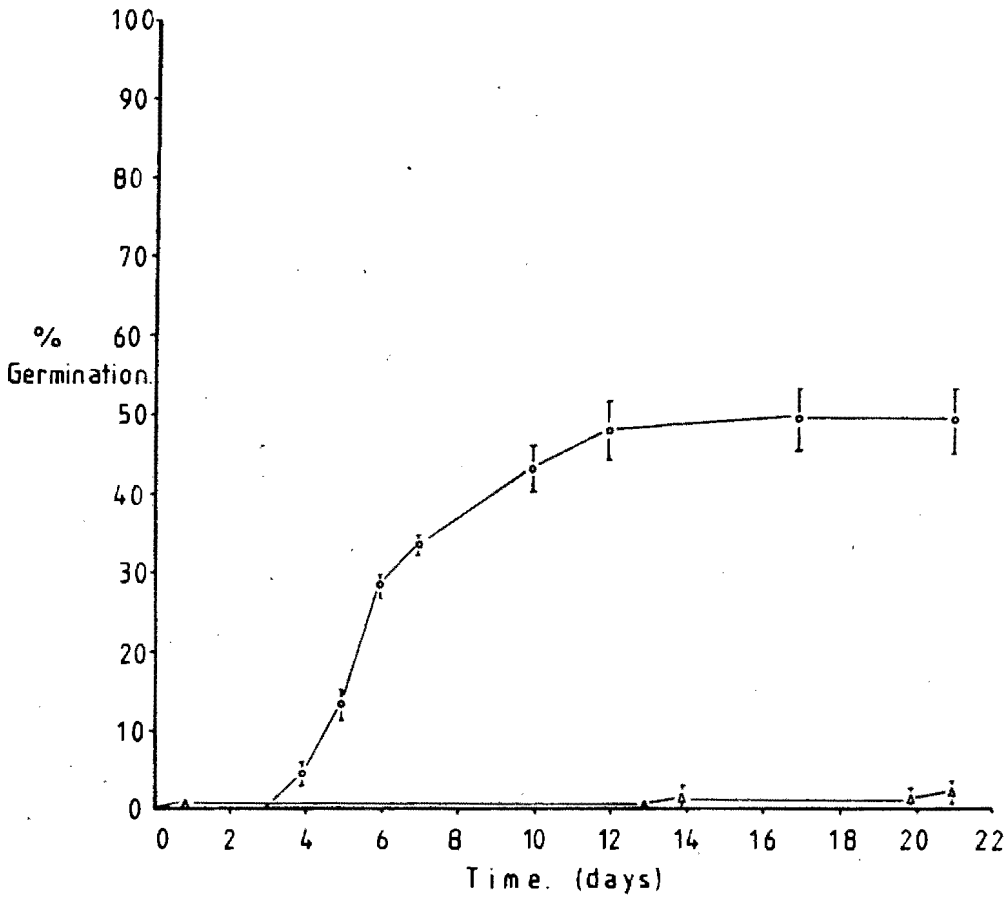


FIGURE 7.3: The effect of the removal of the lemma and palea on the germination of 'hard' fruits from plants found 100m south east of sub-site 1.1. Intact fruits were used as a control.

Control, intact fruits

Caryopses

of the lemma and palea. The results show that there is little difference between the response of this site and that recorded by Joubert (1980) for the Eastern Cape. The removal of the lemma and palea does enhance the germination but at the same time it increases the occurrence of fungal activity.

7.3 THE LEACHING OF FRUITS UNDER RUNNING WATER

Although the removal of the lemma and palea have been shown to enhance germination, no data are available on the state of the lemma and palea in the field, that is, whether or not they are eroded, removed or left intact and in place. It was felt that to use this method of enhancing germination was unsatisfactory without proof of it occurring naturally. Therefore, other methods to enhance the germination were tried.

The high rainfall on Rhodes Estate leads to the possibility of the removal of water-soluble inhibitors by leaching processes. Fruits were exposed to running water for varying periods of time and then used to test the germination performance (See Methods, Section 2.4.2).

7.3.1 Water Leach, Direct to Germination

In many cases the process of leaching the fruits enhanced the rate and percentage germination. In Figure 7.4 the results are shown of leached versus untreated fruits from site 2. The results expressed in this figure are the mean of 12 petri dishes, with 25 fruits per dish. The fruits used were from the three sub-sites of site 2, with 4 dishes of 25 fruits from each site. The mean of the results was calculated and used for Figure 7.4. The leached fruits start germinating sooner and at a higher rate than the non-leached fruits. The final percentage

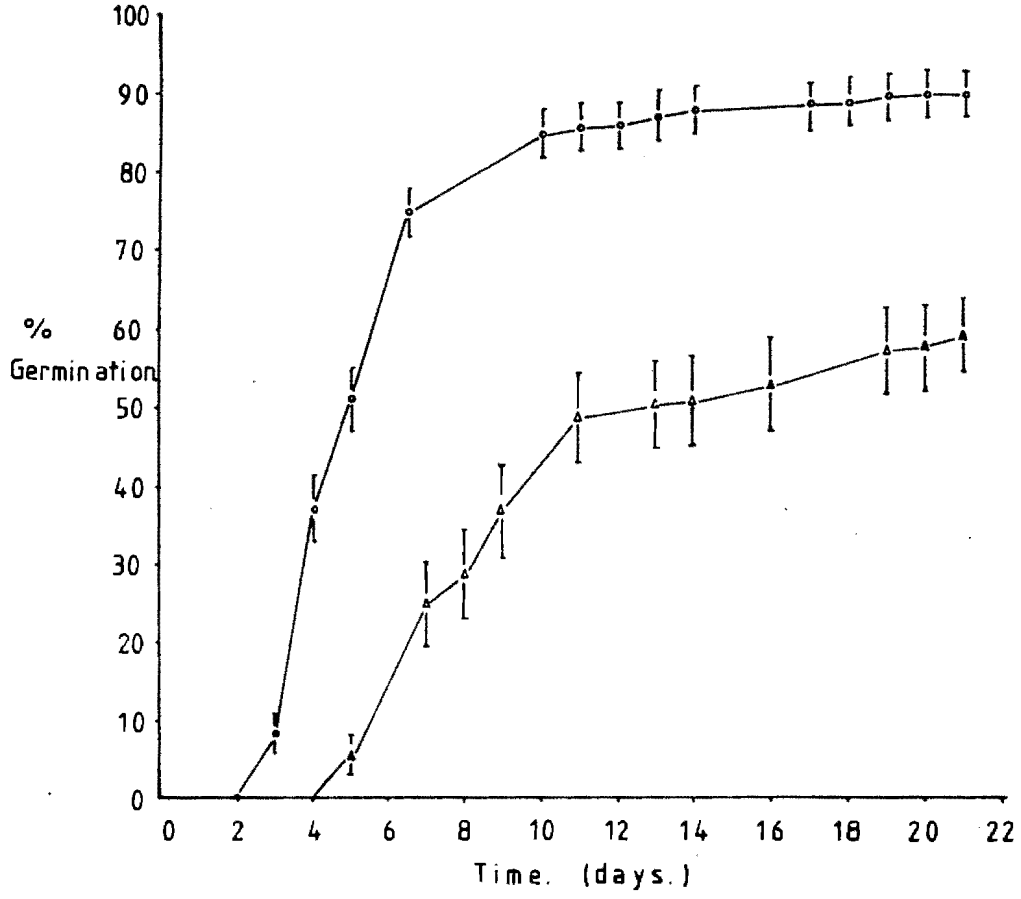


FIGURE 7.4: The germination of fruit from site 2 after being leached for 4 days. Untreated fruits were used as a control. The standard error is shown.

▵ Control, untreated fruits

ρ Fruits leached for 4 days in tap water.

germination in the leached fruits, at 88% is 32% higher than the non-leached control. However, the leached fruits started imbibing 4 days prior to the non-leached fruits. If the control graph is then adjusted, i.e. moved to the left by 4 days so that the initial four days in the petri dish are equated with leaching/imbibing time, then there is little difference between the five samples after 4 days of germination. Differences only become apparent after 5 days and the control did not reach the same levels of germination as the leached fruits.

The experiment was also carried out on fruits from the population about 100 metres South East of sub-site 1.1 (see Section 7.2, Figure 7.3). Leaching was carried out for 5 days as these fruits had been found to be slow germinators. The results are shown in Figure 7.5. When Figure 7.5 is compared to Figure 7.4 it can be seen that the pattern is very similar and that leaching did enhance germination. However, when Figure 7.5 and 7.3 are compared, it can be seen that the two control graphs are significantly different. This occurred even though the conditions during the experiments were identical. From Figure 7.3 the graph of germination of naked caryopses compares favourably with the control of Figure 7.5 in that the rate of germination of naked caryopses is still higher than that of intact fruits. If leached fruits are compared with naked caryopses in these two figures, it is seen that the caryopses show a higher initial rate but lower percentage germination than the leached fruits.

For comparative purposes, the experiment was conducted on fruit from a population at Thomas River in the Eastern Cape. The results were very similar to those found with local fruits (Figure 7.6). The results show that leaching had a consolidating effect on the germination by narrowing the standard error in comparison to that of the control.

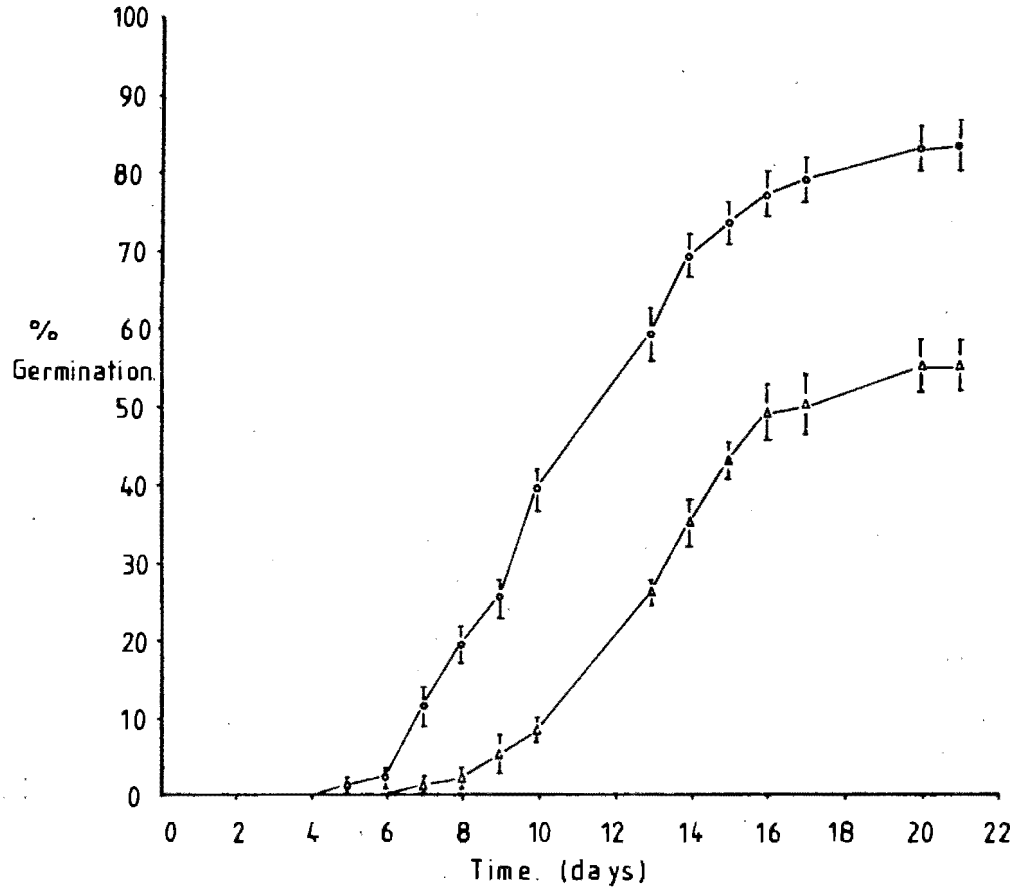


FIGURE 7.5: The germination of fruits from tussocks 100 m south east of sub-site 1.1 after being leached for 5 days. Untreated fruits were used as a control. The standard error is shown.

▲ Control, untreated fruits

○ Fruits leached for 5 days.

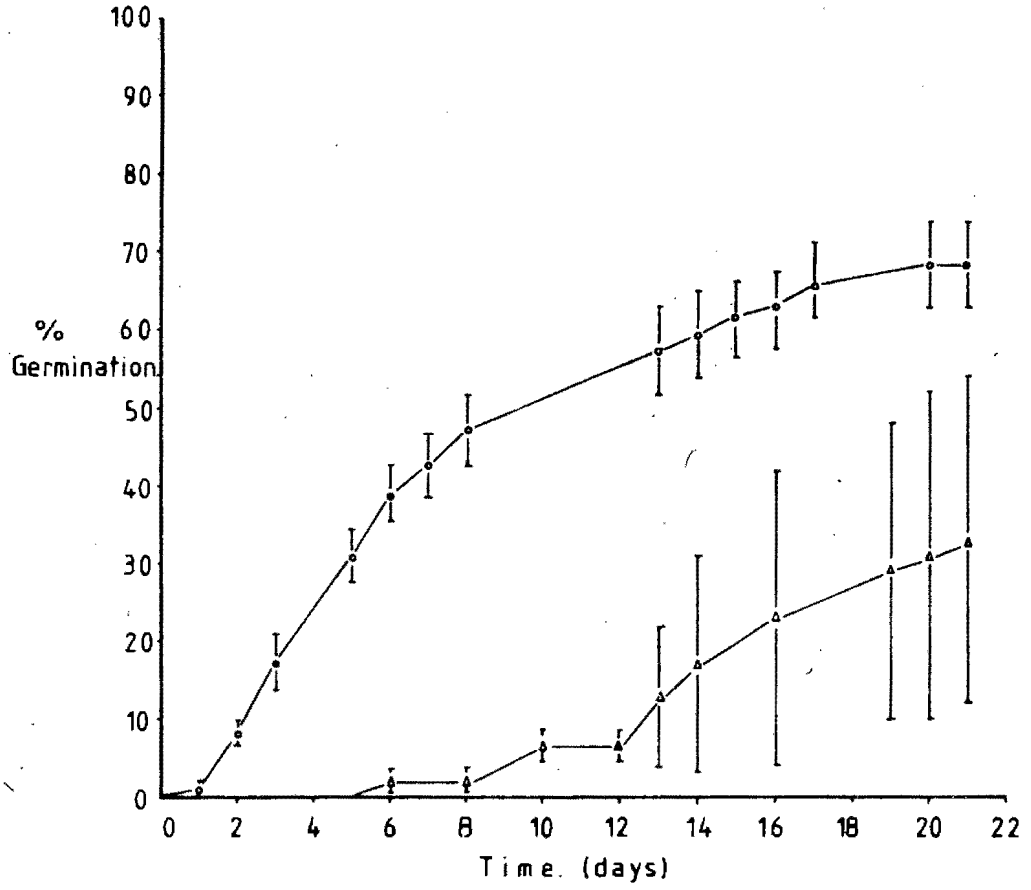


FIGURE 7.6: The germination of fruits from Thomas River after being leached for 4 days. Untreated fruits were used as a control. The standard error is shown.

▲ Control, untreated fruits

○ Fruits leached for 4 days.

The positive effect of leaching on germination proved successful and was used as a standard pre-treatment for most subsequent experiments.

7.3.2 Water Leach, then Storage at 4°C until Germination

The hypothesis of fruits being rain leached and then imbibing water was taken a step further with the question: What if favourable germination conditions don't follow directly after leaching? This is a significant problem in the Western Cape as moisture is most readily available during the cold winter months. Joubert (1980) found that the most rapid germination occurred at a constant 28°C or 12-hourly alternating temperatures of 20 and 10°C. This then means that the fruits are adapted to germinate in the warmer months of spring or summer. To simulate these conditions fruits were first leached and then allowed to dry for about one hour before being placed in sealed glass bottles at 4°C. After approximately one month at 4°C the fruits were placed directly into petri dishes and subjected to the standard germination procedures.

Fruits from sub-site 3.1 were leached for 7 days prior to storage at 4°C. Leached fruits, not subjected to a period of storage, were used as a control. The leached, stored fruits show a higher rate and percentage germination than those not subjected to the intermediate storage (Figure 7.7). The fruits from 4°C storage were partially dried and would presumably require time to re-imbibe. They could, therefore, be expected to have a lower rate of germination than the control. The reason for the stored fruits showing a more rapid germination than the control is unclear. It does, however, show that imbibition followed by unfavourable germination conditions does not decrease the germinability of nassella tussock fruits.

The experiment was repeated, using fruits from sub-site

1.3 and Thomas River, Eastern Cape. The results shown in Figure 7.8 show that the germination of sub-site 1.3 is low which is consistent with results for this site. However, the fruits subjected to the 4°C storage show a lower germination than the control with the difference after 21 days being more than 20%. The fruits from Thomas River show a much higher germination but with a pattern more similar to that of sub-site 1.3 than 3.1, that is, the stored fruits were slower to germinate than the control. However, the difference between the control and the stored fruits is not significant. These results would appear to be more logical than those of Figure 7.7, for the same reasons as discussed for Figure 7.7. These results do confirm that the fruits were not noticeably damaged by being stored after leaching and imbibition.

7.3.3 Alcohol Leach

The results obtained with water leaching suggest the presence of a water soluble inhibitor in the seed coat. Many extraction processes used for the extraction of inhibitors from fruits use alcohol to remove the inhibitor from the source, in this case, from the fruit. It is, therefore, probable that if the fruits were soaked in alcohol, then the inhibitor would be leached from the fruit. An alcohol leach would also serve to sterilize the surface of the fruits. The sterilization of the fruit surface should delay the appearance of any fungi and would, therefore, allow the duration of the experiments to be increased. The possible removal of fungi from the fruit could also alter the germination pattern.

Ethanol at 25% and 50% in water was used for leaching the fruits for 10, 30 and 60 minute periods. For clarity of the graphs, not all the results are shown. Using 25% ethanol and fruits from sub-site 2.3 no change in the

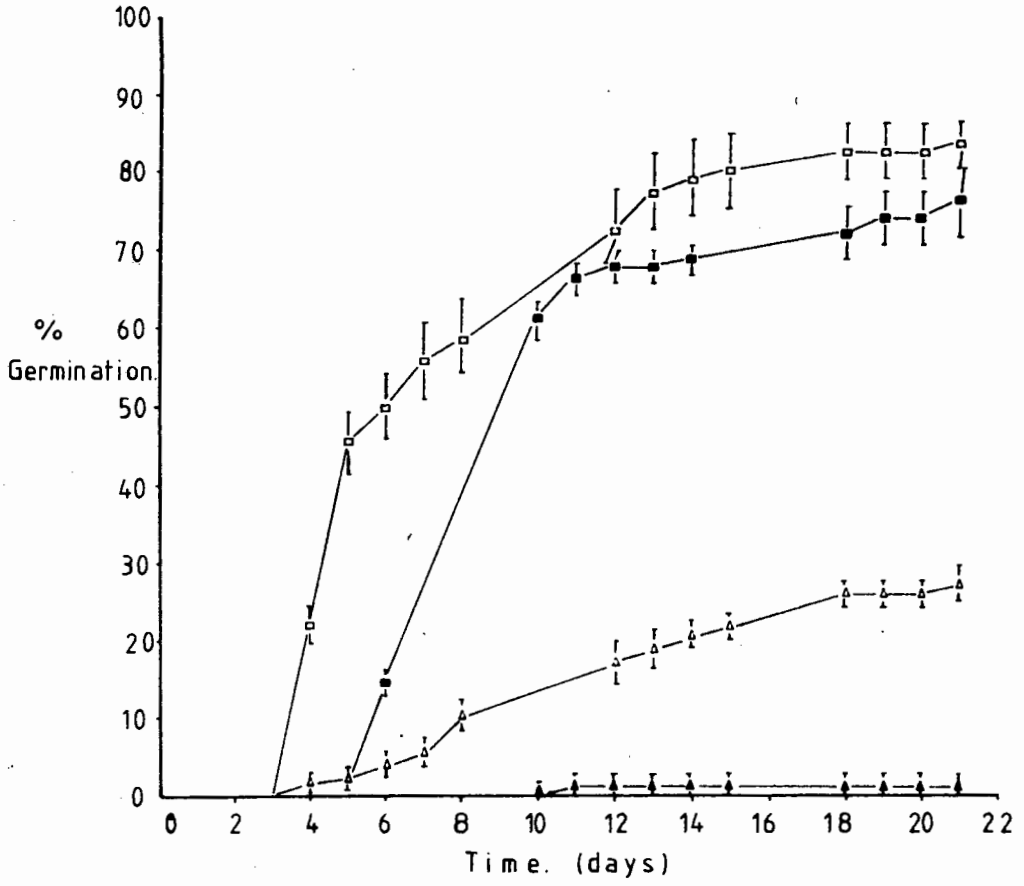


FIGURE 7.8: The germination of fruits from sub-site 1.3 and Thomas River after being leached for 7 days and then stored at 4°C for 1 month.
Leached fruits not put into storage were used as a control.
The standard error is shown.

- ▲ Sub-site 1.3 leached for 7 days, stored at 4°C for 1 month.
- △ Sub-site 1.3 control, leached 7 days
- ■ Thomas River, leached for 7 days, stored at 4°C for 1 month.
- □ Thomas River control, leached 7 days.

germination pattern, in comparison to the untreated control, was noted (Figure 7.9). The results shown are for 10 and 30 minute exposure to the ethanol. These two concentrations of ethanol produced only slightly raised levels of germination. The results from exposure to the ethanol for 60 minutes are very similar except that the standard error is larger and overlaps with the control.

When the ethanol concentration was increased to 50%, there was still no change in the germination pattern. The results are shown in Figure 7.10 with only the 10 minute exposure being shown. This was done as there was complete overlap of the standard errors of all treatments. The only advantage apparent from an alcohol leach is the consolidation of the germination, that is, causing the fruits to germinate more uniformly.

Sub-site 2.3 fruits had been found to germinate readily under most treatments and could therefore have been a poor indicator to use to test the effect of alcohol leaching. Sub-site 1.3 fruits had been found to be more resistant to germination than other sites so fruits from this sub-site were leached in 25% ethanol for 10 and 30 minutes and tested for germination ability. The results shown in Figure 7.11 can be seen to be very similar to those discussed for sub-site 2.3. The only variation is the overall lower rate and percent germination. No significant increase or decrease in the germination was found.

The concentration of alcohol was then increased to 100% and the time of leaching used was limited to one minute. The results expressed in Figure 7.12 show the effect of this on both sub-site 2.3 and Thomas River fruits. The results for the two localities are markedly different. For sub-site 2.3, the alcohol treatment slowed down the initial germination. However, the final percentage germination was slightly higher for the treated fruits.

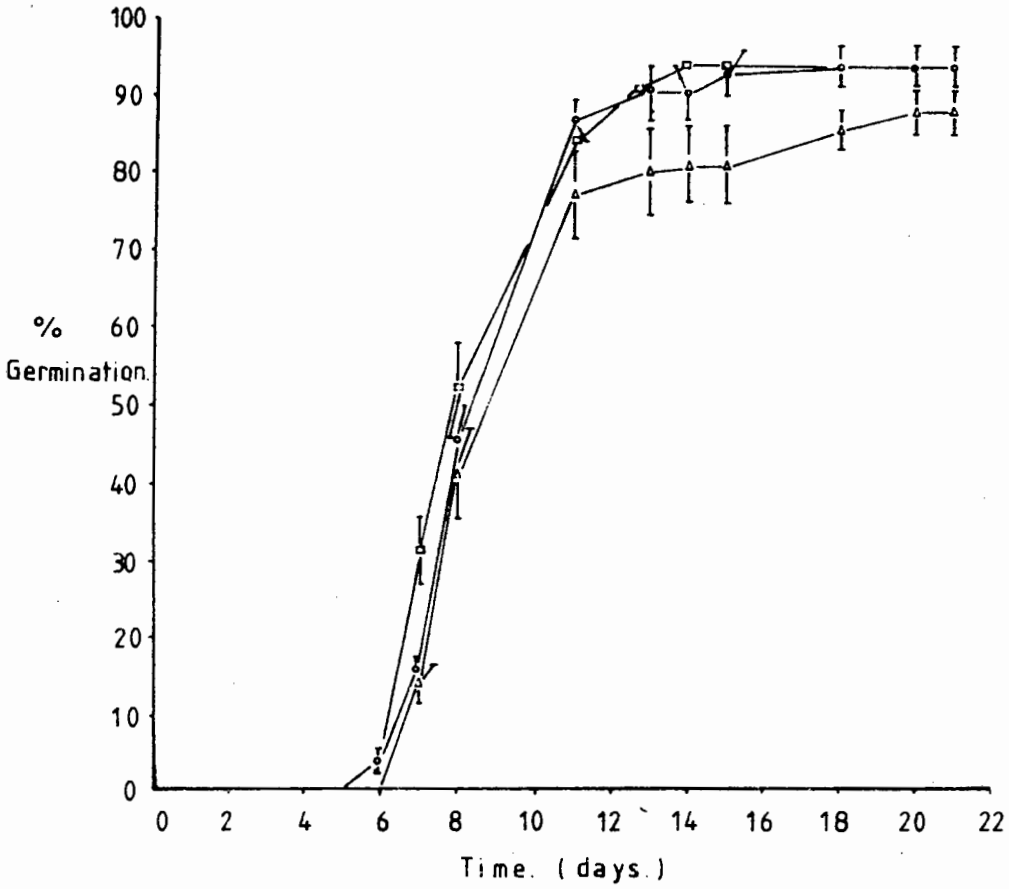


FIGURE 7.9: The germination of fruits from sub-site 2.3 after being leached in 25% ethanol. Untreated fruits were used as a control. The standard error is shown.

▲ Control, untreated

● 25% ethanol for 10 minutes

■ 25% ethanol for 30 minutes.

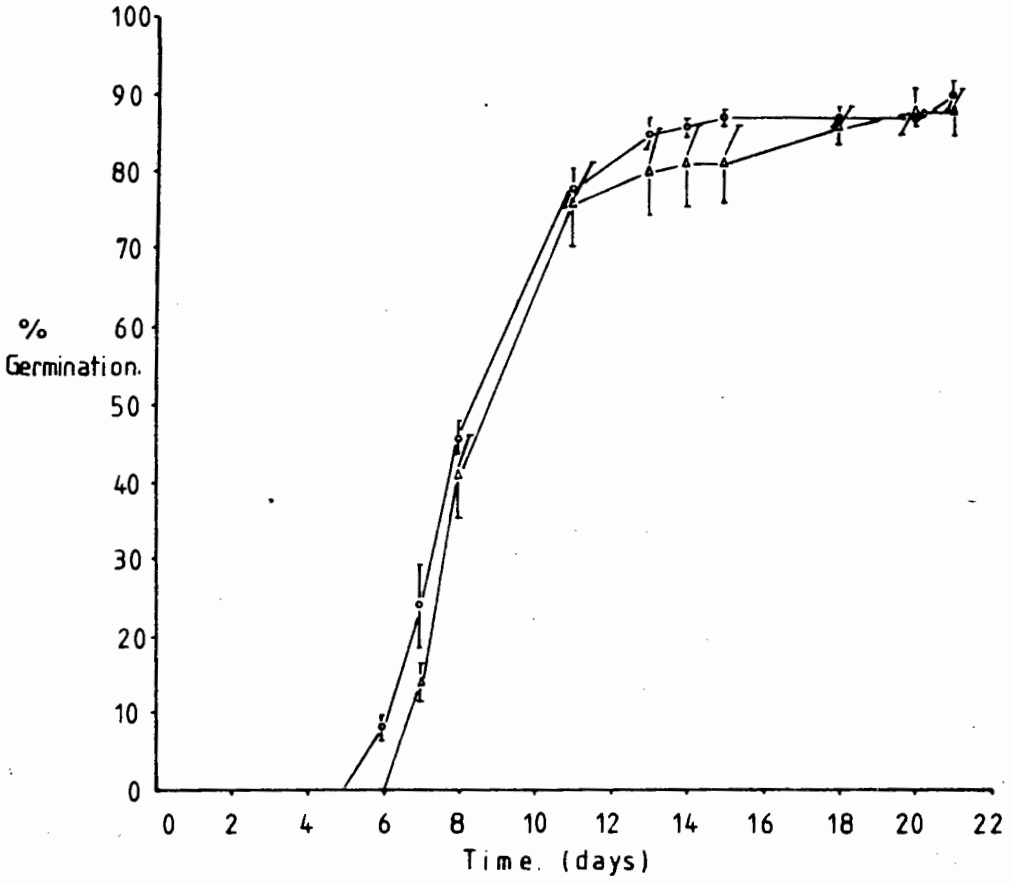


FIGURE 7.10: The germination of fruits from sub-site 2.3 after being leached in 50% ethanol for 10 minutes. Untreated fruits were used as a control. The standard error is shown.

▵ Control, untreated

◦ 50% ethanol for 10 minutes.

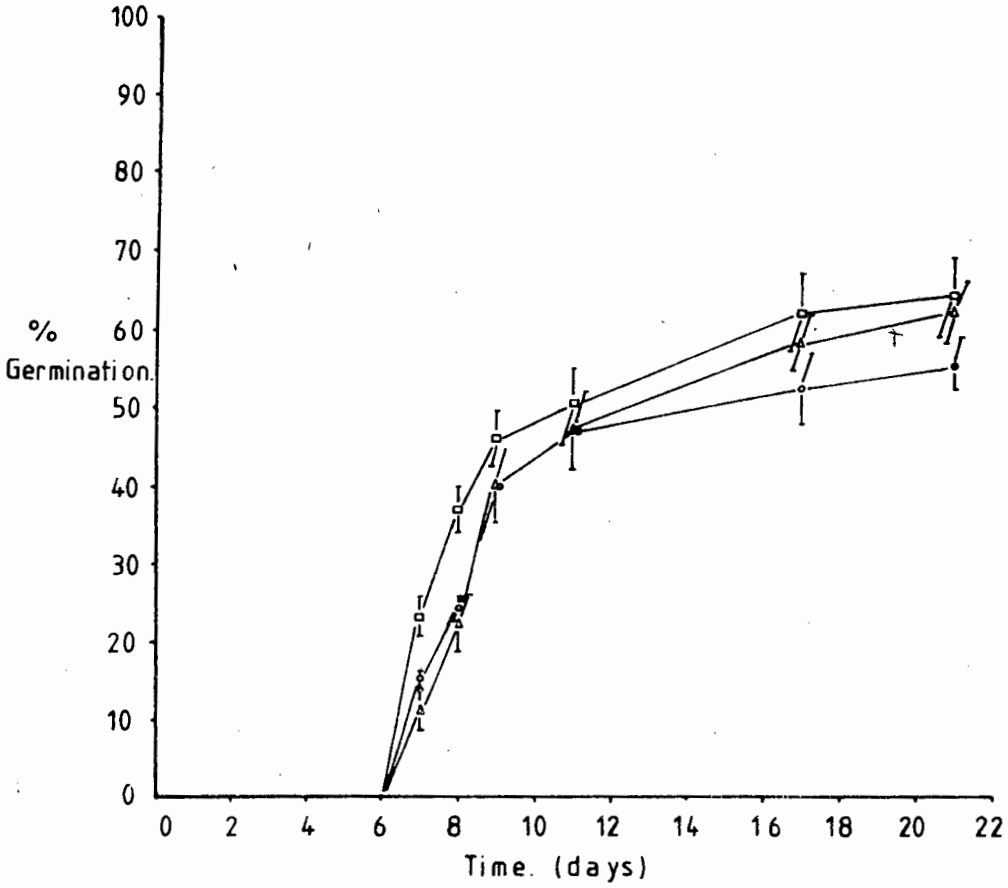


FIGURE 7.11: The germination of fruits from sub-site 1.3 after being leached in 25% ethanol. Untreated fruits were used as a control. The standard error is shown.

- ∘ Control, untreated
- ▵ 25% ethanol for 10 minutes
- ▫ 25% ethanol for 30 minutes.

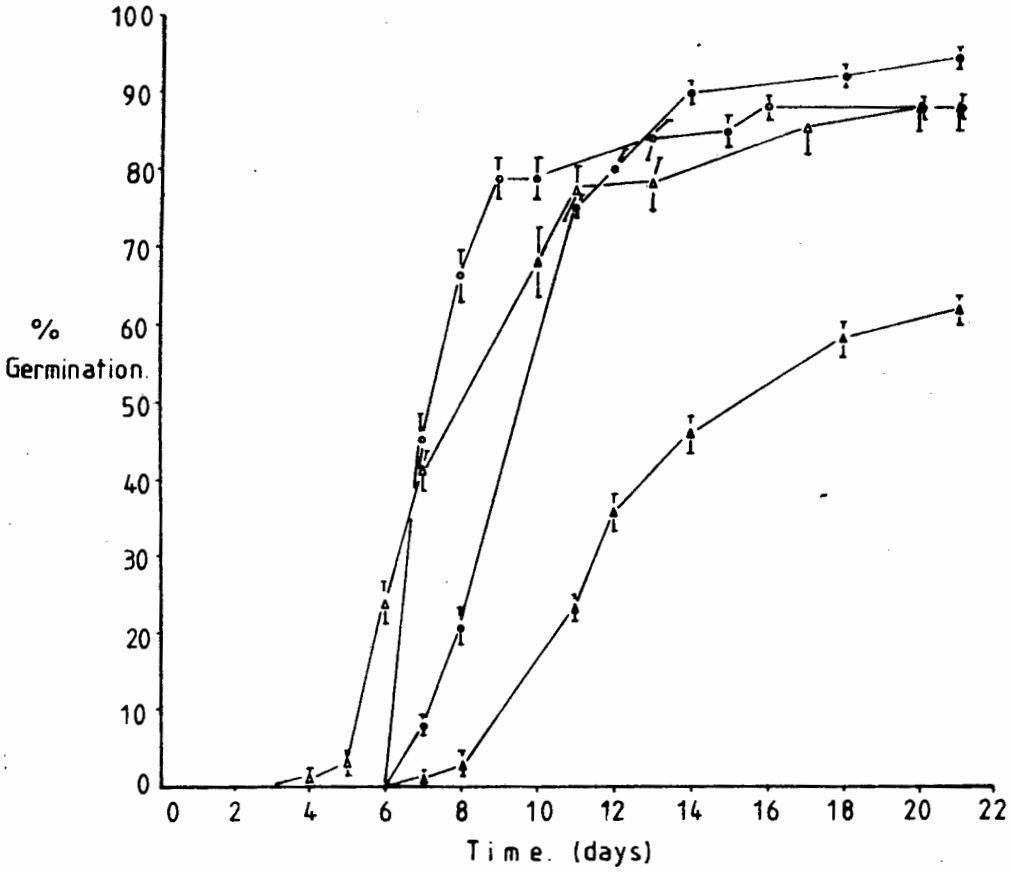


FIGURE 7.12: The germination of fruits from sub-site 2.3 and Thomas River after being leached in 100% ethanol. Untreated fruits from each locality were used as controls.
The standard error is shown.

- ◦ Sub-site 2.3 control, untreated
- • Sub-site 2.3, leached in 100% ethanol for 1 minute
- ▵ Thomas River control, leached in water for 4 days
- ▲ Thomas River, leached in 100% ethanol for 1 minute.

With the Thomas River fruits the situation is that the water leached control shows its normal high rate of germination while the alcohol leached fruits showed a significantly lower rate and final percentage germination.

These results still do not confirm either an increase or decrease in the germination performance of nassella tussock fruits with alcohol leaching. It can only be concluded that the concentrations of ethanol and times of exposure used do not stimulate the germination of nassella tussock.

As a final experiment with alcohol leaching, naked caryopses of sub-site 2.3 were leached in 25% ethanol for 10 minutes. This treatment had no effect on the germination performance of the caryopses. The only result of importance is that 10 minutes in 25% ethanol delayed the appearance of fungal growth on the germinating caryopses.

7.4 OPTIMUM GERMINATION TEMPERATURE

The temperature requirements for nassella tussock germination in the summer drought-winter rainfall region may be different to that of the nassella tussock in the summer rainfall climate of the Eastern Cape. These experiments, on the temperature requirements for the germination of nassella tussock were carried out on a thermogradient bar. The construction of the bar was discussed in Section 2.4.5.

7.4.1 NAKED CARYOPSES

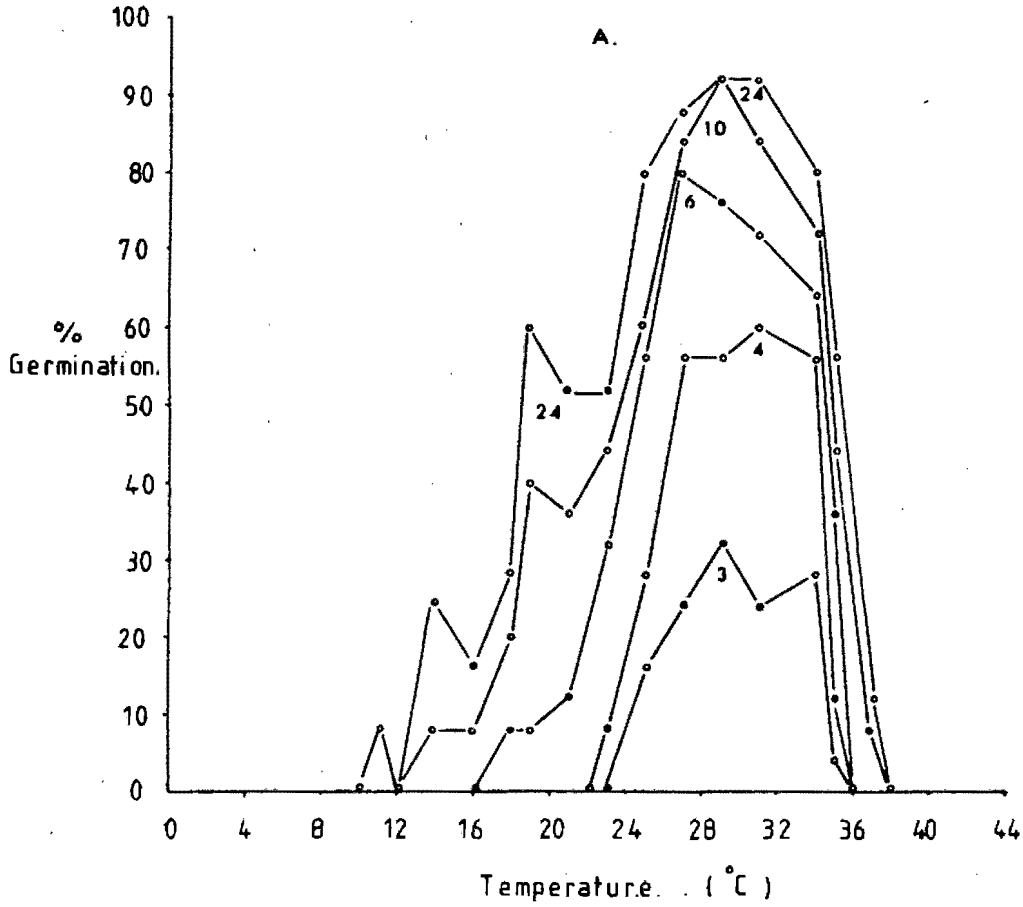
Naked caryopses, fruit from which the lemma and palea had been removed, were used because the germination rate of the intact fruits was found to be very low. Twenty-five caryopses were placed at either 1 or 2°C intervals along

the thermogradient bar. The temperature range of the bar was set from 5 to 50°C. Counting was undertaken at regular intervals, decided upon by the rate of germination. A caryopsis was removed once it had germinated and been counted. Caryopses from both sub-sites 1.3 and 2.3 were used.

The results of sub-site 1.3 are shown in Figure 7.13. In Part A of Figure 7.13 the results are expressed as temperature against percentage germination. The results are cumulative with each line representing the number of caryopses that had germinated at each temperature on the specified day. The number below each graph shows the number of days elapsed since the initiation of the experiment. Figure 7.13 A shows the optimum temperature to fluctuate between 26 and 30°C. The rate of germination is high, with 50% germination being reached between 26 and 34°C after only 4 days. The maximum germination of 92% was achieved after 10 days at 28°C.

Figure 7.13 B shows the same results as in Figure 7.13 A expressed in a simplified form, defined as the character curve (Thompson, 1973). For this graph the results are plotted with temperature against 'time to 50% germination'. The 50% germination is 50% of the maximum germination obtained irrespective of temperature, in this case 92%. The character curve gives an approximate curve which indicates the optimal temperatures as well as the upper and lower limits of the temperature requirements. The delay to germinate and the rate of germination are also shown. For sub-site 1.3 the optimal temperature can be seen to be between 26 and 32°C. After 24 days no significant germination was found below 18°C or above 35°C (Figure 7.13 B). This shows a high rate of germination over a relatively narrow temperature range.

FIGURE 7.13: The temperature requirements of caryopses from sub-site 1.3. (A) The germination of caryopses on days after sowing. The numbers below the lines show the time, in days from sowing. (B) The character curve, drawn from data of part A, The upper and lower asymptotes have been drawn because less than 50% germination was obtained after 26 days beyond these temperatures. The right hand end of the curve, although drawn on 1 point, would have another point at 36°C somewhere after 26 days.


A.
% Germination.
Temperature. (°C)
24
10
6
4
3
24
0
4
8
12
16
20
24
28
32
36
40
44
0
10
20
30
40
50
60
70
80
90
100

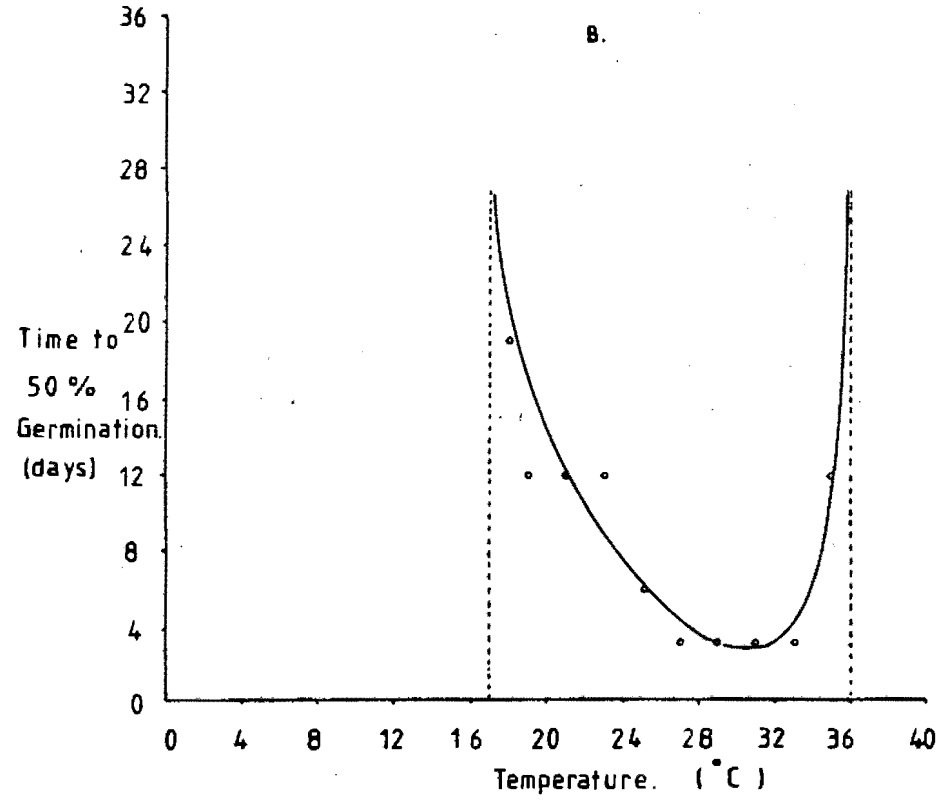
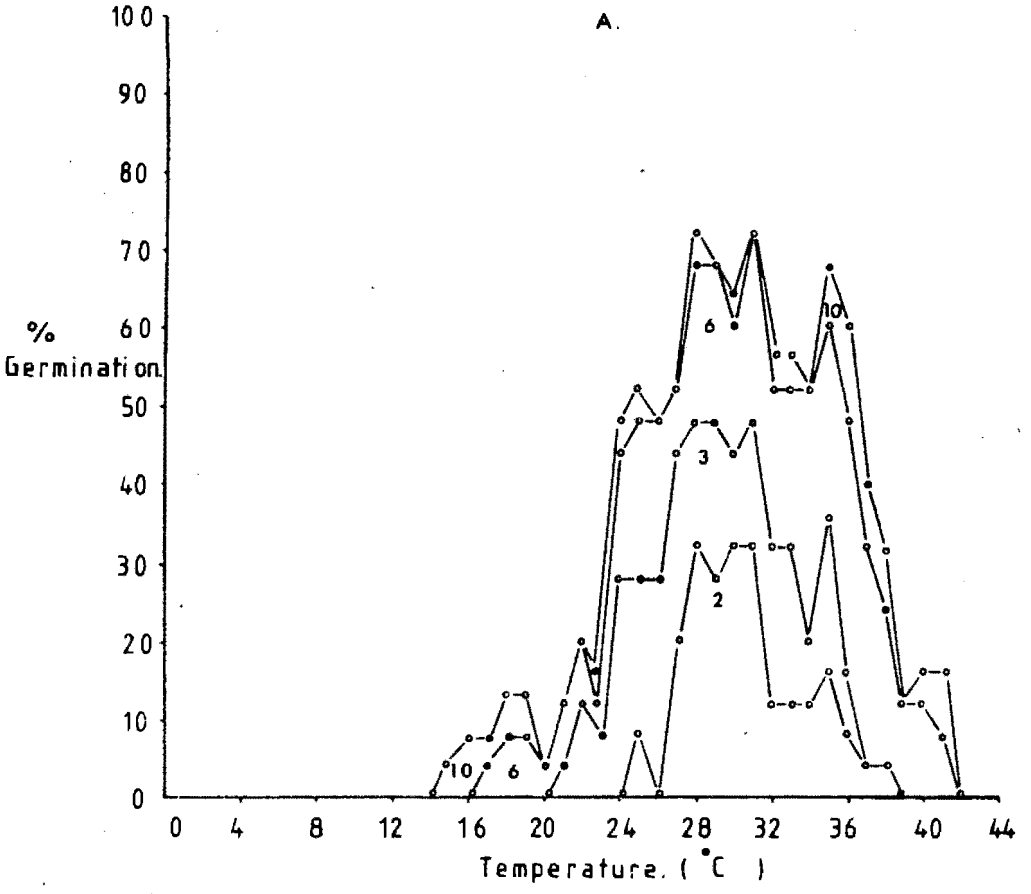

B.
Time to 50 % Germination. (days)
Temperature. (°C)
0
4
8
12
16
20
24
28
32
36
40
0
4
8
12
16
20
24
28
32
36

FIGURE 7.14: The temperature requirements of caryopses from sub-site 2.3. (A) The germination of caryopses on days after sowing. (B) The character curve for the same sub-site. The asymptotes have been drawn for the same reasons as discussed in Figure 7.13.


A.
100
90
80
70
60
50
40
30
20
10
0
% Germination
10
6
6
3
2
10
0 4 8 12 16 20 24 28 32 36 40 44
Temperature. (°C)

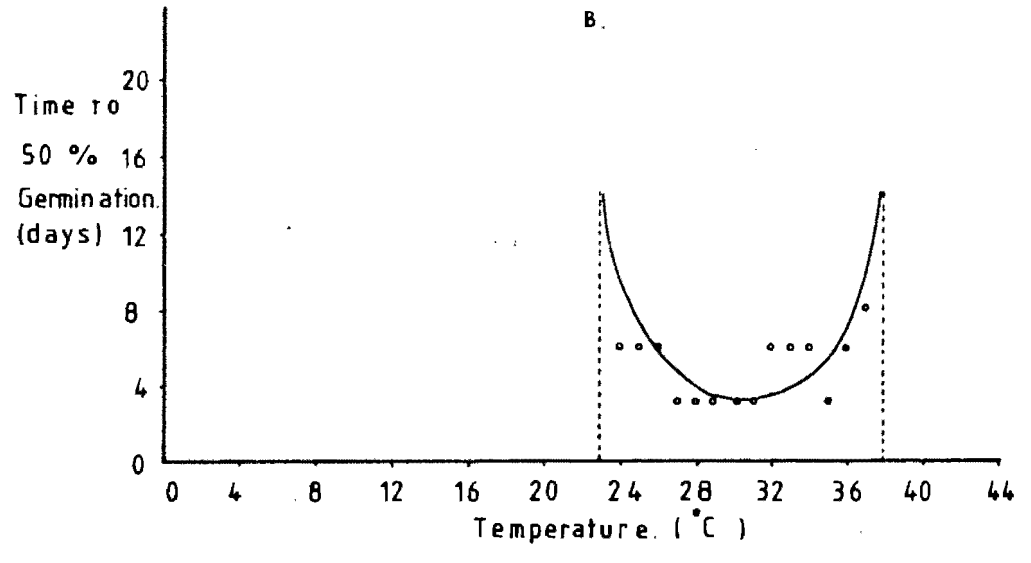
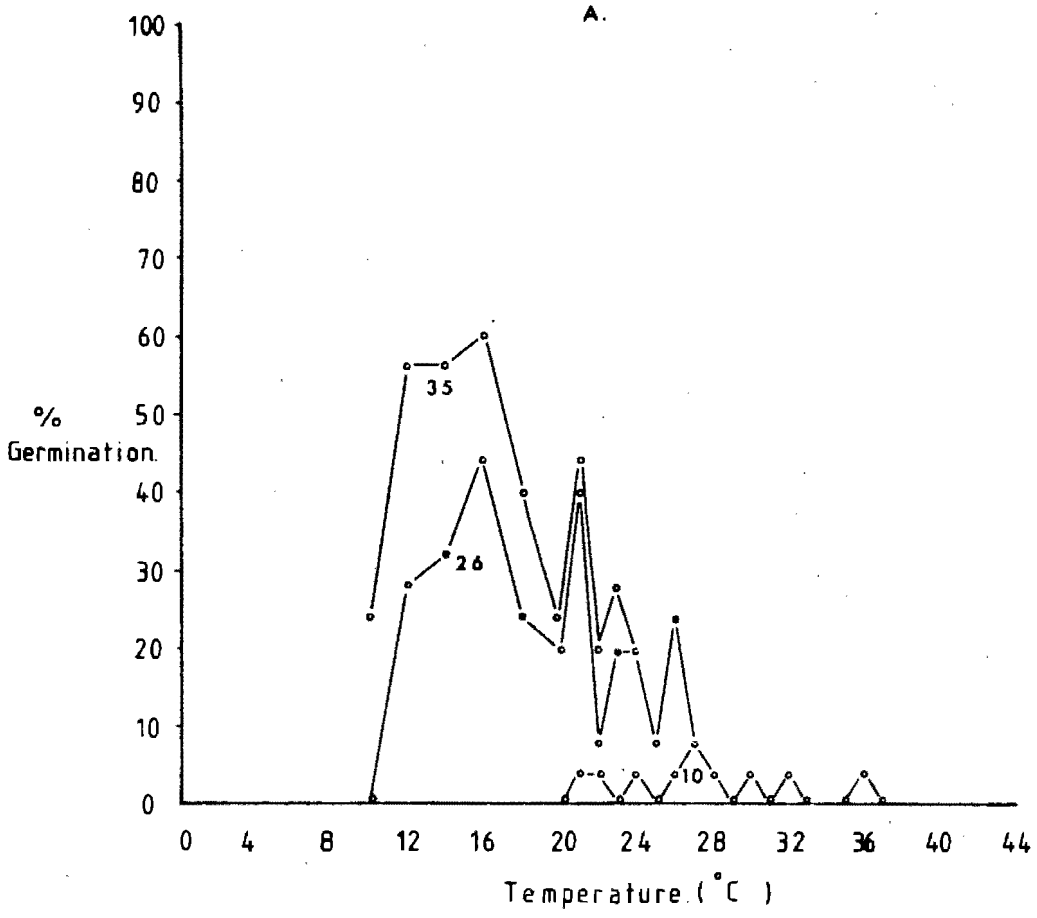

B.
20
16
12
8
4
0
Time to 50 % Germination. (days)
0 4 8 12 16 20 24 28 32 36 40 44
Temperature. (°C)

FIGURE 7.15: The temperature requirements of leached fruits from sub-site 1.3. (A) The germination of fruits on days after sowing. (B) The approximate character curve for leached fruits from sub-site 1.3. Only 5 points and the two asymptotes were obtained after 38 days germination. The curve shown is felt to be the probable shape. The important features are tne delay to germination (26 days) and the shift to the left, i.e. colder optimum temperatures (cf. Figure 7.13).


A.
100
90
80
70
60
50
40
30
20
10
0
% Germination.
35
26
10
0 4 8 12 16 20 24 28 32 36 40 44
Temperature. (°C)

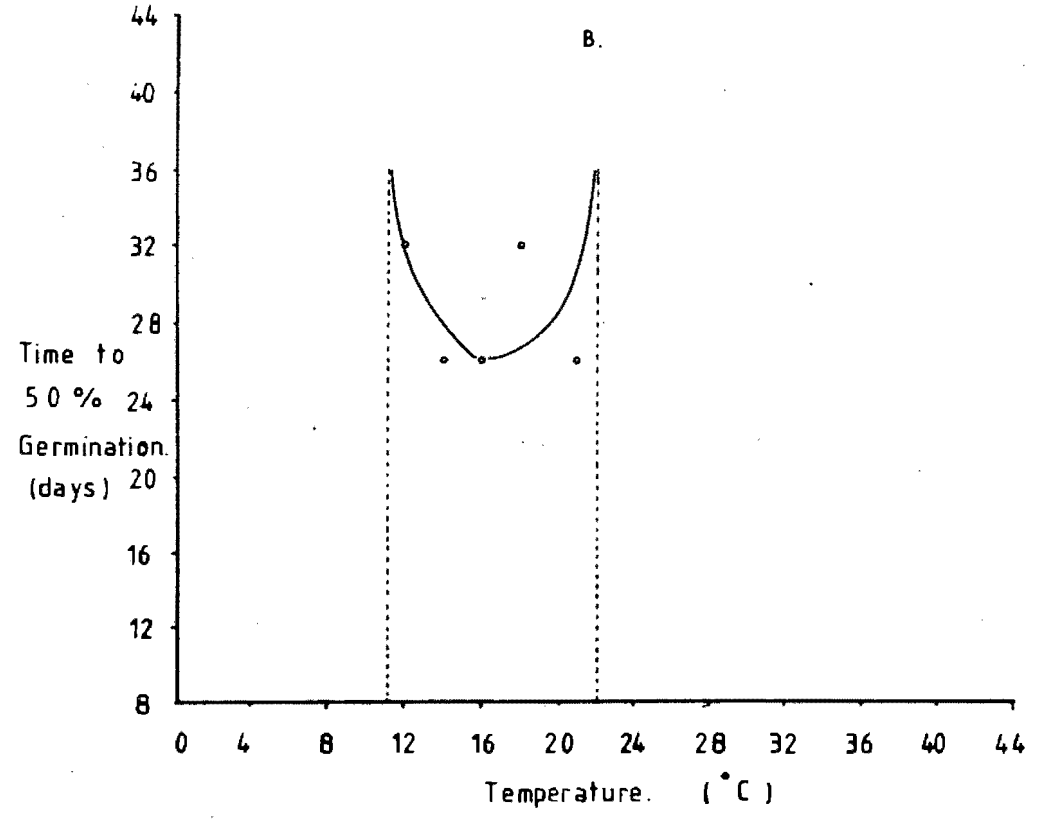
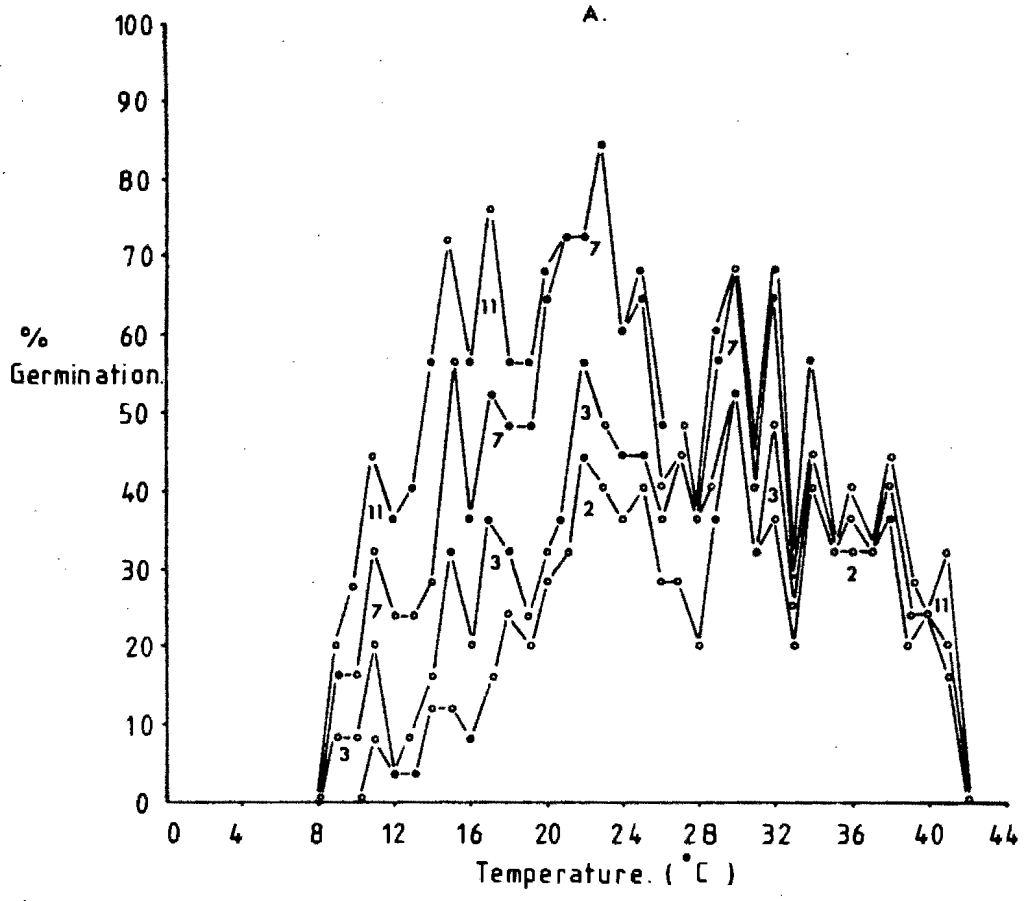
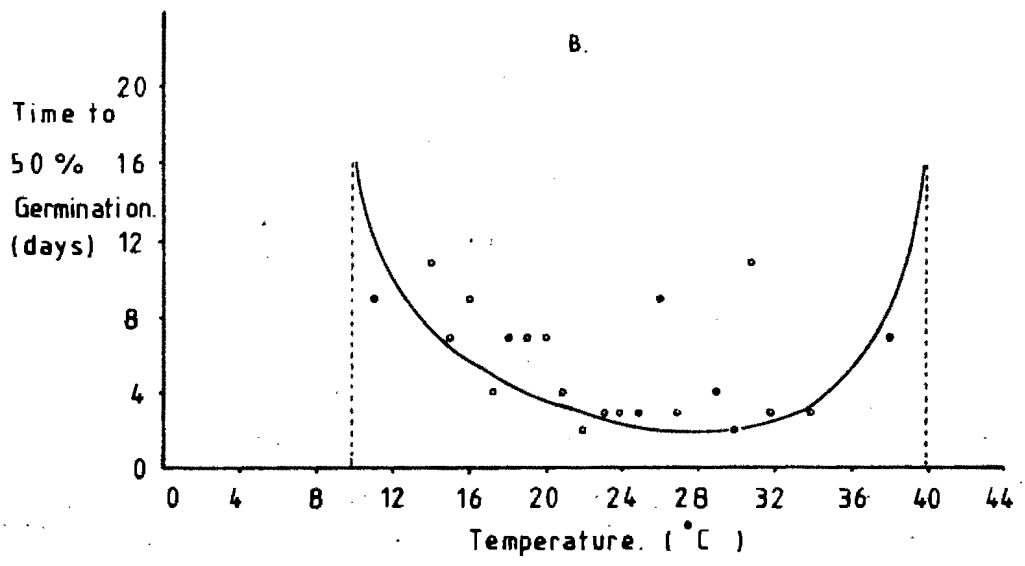

B.
44
40
36
32
28
24
20
16
12
8
Time to 50 % Germination. (days)
0 4 8 12 16 20 24 28 32 36 40 44
Temperature. (°C)

FIGURE 7.16: The temperature requirements of leached fruits from sub-site 2.3. (A) The germination at days after sowing. (B) The character curve for leached fruits from sub-site 2.3.


A.
100
90
80
70
60
50
40
30
20
10
0
% Germination.
0 4 8 12 16 20 24 28 32 36 40 44
Temperature. (°C)
11
7
3
2


B.
20
16
12
8
4
0
Time to 50 % Germination. (days)
0 4 8 12 16 20 24 28 32 36 40 44
Temperature. (°C)

be from 22°C to 34°C, with the upper and lower limits being 40°C and 10°C respectively. The delay to germination of 2 days is short.

Figure 7.16 B covers the range of the curves for both sub-sites' naked caryopses germination.

Using Thompson (1973) as a guide it would appear that nassella tussock is unsuited to a Mediterranean climate. Figure 7.17 shows a character curve, typical of a Mediterranean species (Thompson 1973). If this is compared to Figures 7.13 B, 7.14 B and 7.16 B, then it is clear that the optimum temperature requirements of nassella tussock are too high for a Mediterranean type climate. Only Figure 7.14 B and part of 7.16 B show the required temperatures. Thompson (1973) suggests that the milder a winter, the lower the optimum temperature requirements and that Mediterranean species can be expected to have lower minimum and maximum requirements.

The normal annual temperature range of a typical Mediterranean type climate is given as between 10°C and 22°C (Kendrew, 1937). This temperature range coincides with the milder temperatures required for a plant adapted to a Mediterranean type climate (Thompson, 1970 and 1972). If this temperature range is used it is clear that only a limited portion of the fruits from Rhodes Estate are adapted to the climate. However, the temperature data for Rhodes Estate (Section 8) shows that this area has higher summer means. These temperatures reach monthly means of 30°C, with daily maxima as high as 36°C. The temperature requirements of Rhodes Estate fruits are therefore similar to those recorded in the field.

Nassella tussock is not ideally suited to a Mediterranean type climate with moderate summer temperatures. From the field data (Section 8) it appears that Rhodes Estate

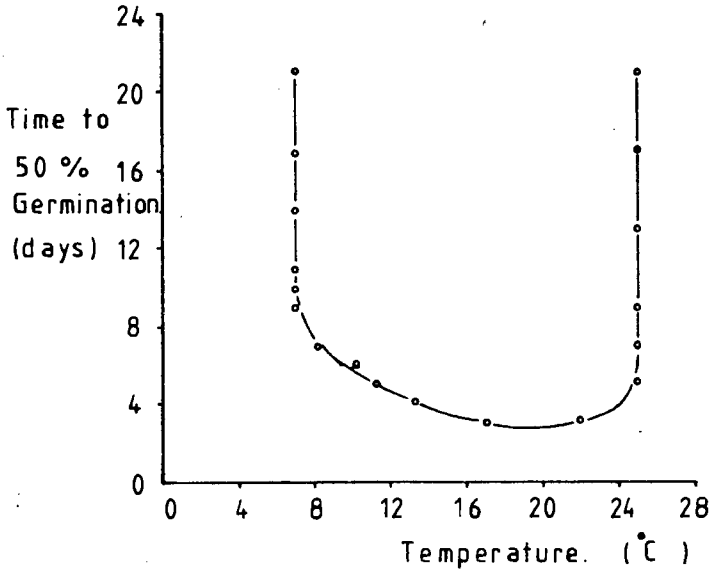


FIGURE 7.17: The character curve of Silene italica L. Pers which is stated by Thompson (1973) as showing the typical character curve of plants adapted to a Mediterranean type climate. (Redrawn from Thompson, 1973).

has higher mean summer temperatures than other Mediterranean type areas. This, therefore, means that nassella tussocks temperature requirements for germination are adapted to the temperature régime of Rhodes Estate.

7.5 BIOASSAY FOR INHIBITORS IN THE FRUIT

7.5.1 A Simple Bioassay for the Presence of Inhibitors

Five grammes of fruits from sub-site 1.3 were ground with a mortar and pestle in about 50 mℓ of distilled water. This was left for an hour with periodic stirring and then double filtered through Whatman No. 1 filter paper. The filtrate was then used as the germination liquid, in place of distilled water, for caryopses and leached fruits.

Fruits from sub-site 2.3 were leached for 4 days and then placed in 8 petri dishes. The extract was added to 4 of the dishes and distilled water to the other 4 to serve as a control. The leached control showed the typical high rate of germination with 85% germination being obtained in 7 days (Figure 7.18). The final percentage germination was 93%. In contrast the leached fruits with extract showed a markedly lower rate of germination with only 69% germination after 7 days. However, the control produced a smooth curve throughout the germination time while the fruit plus extract produced a false slowing down phase after 3 days. The rate did increase again (Figure 7.18). Differences are clear between the two graphs up to the 10th day but from this point on there is little to distinguish between them. After 21 days the leached fruit plus extract had produced 88% germination against the 93% of the control. There is no overlap in the standard errors of these two graphs.

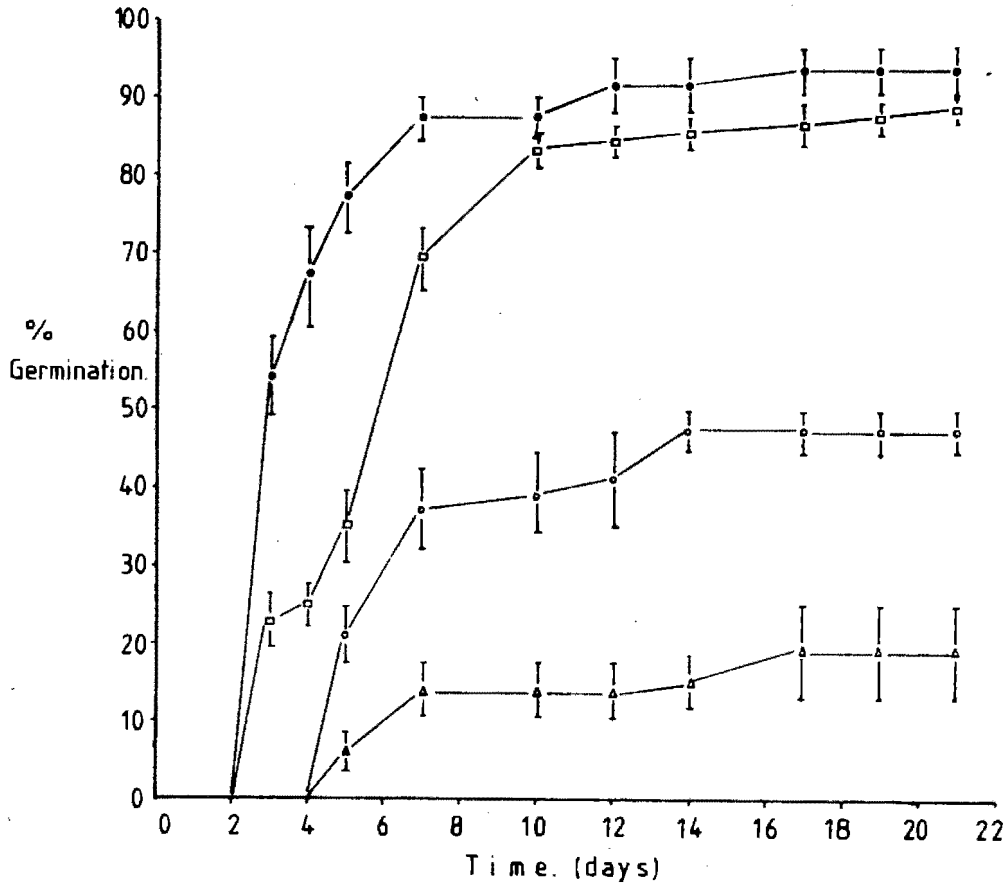


FIGURE 7.18: The germination of fruits and caryopses of sub-site 2.3 on extracts of fruits from sub-site 1.3. Caryopses and leached fruits germinated in distilled water were used as controls.
The standard error is shown.

▵ Sub-site 2.3 caryopses plus extract.

◦ Sub-site 2.3 caryopses, control

▫ Sub-site 2.3 fruits leached for 4 days, plus extract.

• Sub-site 2.3 control, leached fruits.

Naked caryopses of sub-site 2.3 were subjected to the same treatment as the intact fruits, minus the 4 day leaching. The results shown in Figure 7.18 show that although the control germination is relatively low, the addition of fruit extract decreases both the rate and percentage germination. The addition of the fruit extract increased the occurrences of fungal growth but only from day 17.

The experiment was repeated, using extracts made up from caryopses and the separated lemmas and paleas. The extracts were prepared as described above but only 2,5 g in place of 5 g were used. Only naked caryopses were germinated in this assay. The experiment was terminated after 10 days as all samples had reached the plateau phase of germination and fungal activity was increasing. The control germination at 50% is again lower than normal (Figure 7.19). With the addition of caryopses extract the rate of germination decreased slightly as did the percentage germination. The addition of the lemma and palea extract caused the greatest decrease in both rate and percent germination. This produced a final germination figure of 30% against the 50% of the control.

The results of both these experiments point to the presence of an inhibitor in the nassella tussock fruits. The results shown in Figure 7.19 suggest the probable locality to be the fruti coat, the lemma and palea. The fact that the fruits show a higher germination than naked caryopses contradicts this hypothesis as there would still be inhibitor present in the lemma and palea after leaching. However, this difference is more likely due to the fact that the removal of the lemma and palea must damage the caryopses. The naked caryopses were checked for damage before use but it is obviously not possible to detect all damaged caryopses. A second factor that is probably contributory to the lowered germination of the naked caryopses is their susceptibility to fungal attack. This

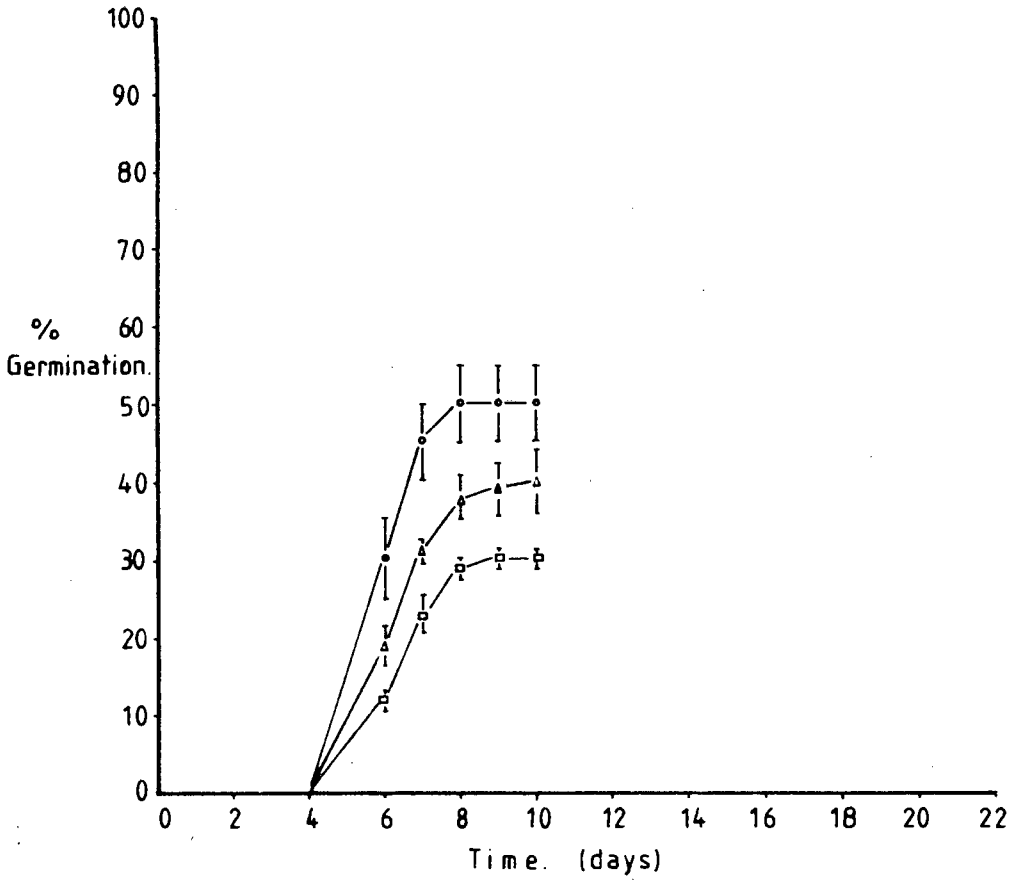


FIGURE 7.19: The germination of caryopses of sub-site 2.3 on caryopses extracts and lemma and palea extracts. Caryopses, germinated in distilled water were used as a control.
The standard error is shown.

- ∘ Sub-site 2.3 control
- ▵ Sub-site 2.3 caryopses plus caryopses extract.
- ▫ Sub-site 2.3 caryopses plus lemma and palea extract.

is increased by the addition of the extracts which no doubt serves as a growth medium for the fungi. It is felt that the pattern, more than the percentages, is the important factor. If this is taken into account, then the presence of an inhibitor seems likely.

7.5.2 A Bioassay for Inhibitors using Chromatographic Methods

The positive results achieved with the simple bioassay described above led to a more refined assay making use of chromatographic techniques. Naked caryopses placed on the Rf strips of chromatography paper were placed in petri dishes and germinated (Methods Section 2.4.11.1). The results are shown in Figure 7.20 A to F. The graph with circular points is the control in all the figures with the others being the germination at the different Rf values. Figure 7.20 A, B and C show the germination on Rf 1, Rf 2 and Rf 3 respectively. The graphs with triangular points in D and E are for Rf 4 and 5 respectively. All the germination on Rf 1 to Rf 5 showed only slight stimulation of germination, as for Rf 2 (Figure 7.20B) or none at all, Rf 5 (Figure 7.20 E). The germination on Rf 6 (squares in Figure 7.20 E) and Rf 7 (triangles, Figure 7.20 F) produced marked decreases in the germination of the caryopses. At both these Rf values the germination was consolidated with most caryopses germinating at similar times. At Rf 8 (Figure 7.20 E, squares) the germination was less than the control but greater than that on Rf 7. The germination on Rf 9 (squares, Figure 7.20 D) was also lower than the control. On both Rf 8 and Rf 9 the standard error was large. The results of the germination on Rf 10 were not plotted. The results of Rf 10 showed low germination but with very large standard errors. These results again back the probability of an inhibitor (Rf 6, Rf 7, Rf 8 and Rf 9) while Rf 1, Rf 2 and Rf 3 point to the possibility of a germination stimulator. The identity and locality of the inhibitor was not investigated

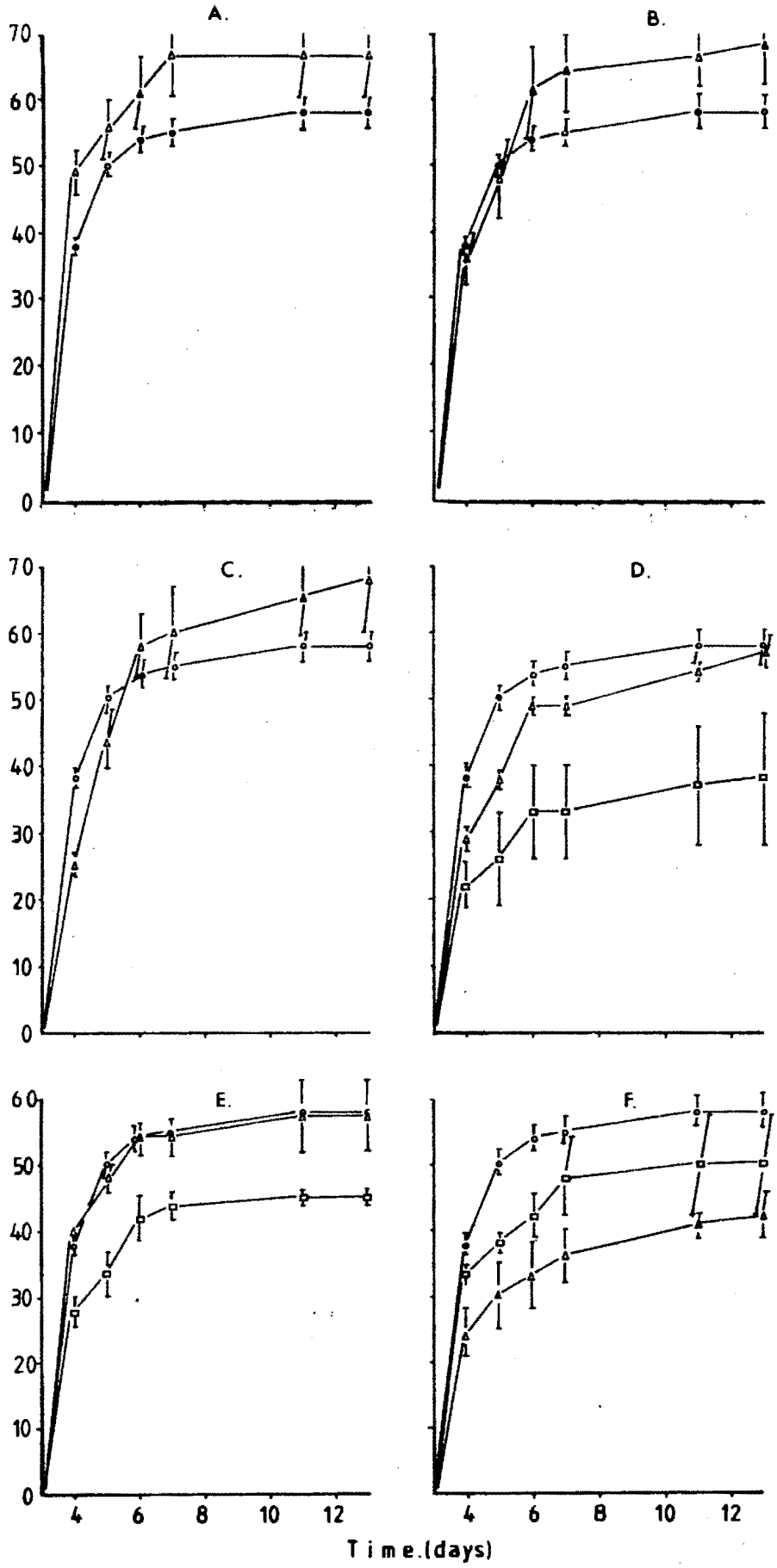
FIGURE 7.20: The germination of naked caryopses from sub-site 2.3 on Rf strips used to investigate the presence of an inhibitor. The standard error is shown.

(A) ▵ Rf 1; (B) ▵ Rf 2; (C) ▵ Rf 3;

(D) ▵ Rf 4, ▫ Rf 9; (E) ▵ Rf 5, ▫ Rf 6;

(F) ▵ Rf 7, ▫ Rf 8.

In all sections (•) is the control which was caryopses germinated on a blank chromatogram.


A.
B.
C.
D.
E.
F.
70
60
50
40
30
20
10
0
4
6
8
10
12
T i m e.(days)

as it was felt that this could develop into a project of its own. From leaching experiments, the removal of the lemma and palea and the experiments with extracts described above, it seems clear that a germination inhibitor is present. The available results suggest that this inhibitor is most probably located in either the lemma or palea or both.

7.6 THE EFFECT OF BURNING ON THE GERMINATION OF NASSELLA TUSSOCK FRUITS

Once an area infested with nassella tussock or well supplied with its fruits is burnt, the germination of the nassella fruits is high. The subsequent growth of nassella tussock seedlings is dense suggesting that the burn, in some way, stimulated the germination of the fruits. One way for this to occur is for the heat of the burn to affect the fruits so as to decrease an inhibitor action or to physically break down the lemma and palea. To test this, fruits were artificially heated in the laboratory in an attempt to simulate the effect of a burn.

7.6.1 The Effect of Dry Heat on Germination

The most obvious effect of fire on fruits would be the direct burning of fruits exposed either on the ground or still attached to the tussocks. The temperatures found in a grass burn by Daubenmire (1968) are shown in the methods section, 2.4.4. These temperatures would apply mostly to fruits attached to the tussocks. The temperature for fruits on the soil surface would depend largely on the amount of litter. The temperatures in any burn are likely to fluctuate depending on the amount of combustible plant material and litter. These fruits would, however, experience a dry heat as they would be exposed directly to the flames. This was simulated in the laboratory by placing fruits in a muffle furnace.

Once the fruits had been exposed to the heat treatment they were subjected to the standard germination procedures (Section 2.4.1). After 21 days only one sample had started to germinate and then only to 2% (Figure 7.21). The experiment was extended and only after 28 days did germination occur. The temperature that produced the highest germination was 100°C for 60 seconds. At this temperature germination started on the 20th day and by the 28th day had reached 80%. Exposure to 200°C for 60 seconds produced 45% and 30 seconds at 300°C gave 30% germination after 28 days. Exposure to 400°C for 15 seconds resulted in no germination. The fruits used in this experiment were from sub-site 2.3 which has been shown to have a very high rate of germination. The results do not agree with field observations that burning enhances germination. Not only did this heat treatment substantially reduce the germination but it also resulted in an increase in the standard errors. This increase in standard error suggests that the process of heating the fruits has in fact damaged them and thereby caused the staggered germination.

7.6.2 The Effect of Steaming on the Germination Performance of Nassella Tussock Fruits

No work has been done on the size of the nassella tussock seed store buried in the ground. It is logical, due to the high fruit production, that this store must be large and so play an important role in the re-establishment of nassella tussock populations. The germination of fruits after a burn could, therefore, be from this buried store and not from the above ground fruits. If these buried fruits are affected by a burn, their depth of burial would chiefly determine the temperature to which they would be subjected. Being buried, the moisture content of the

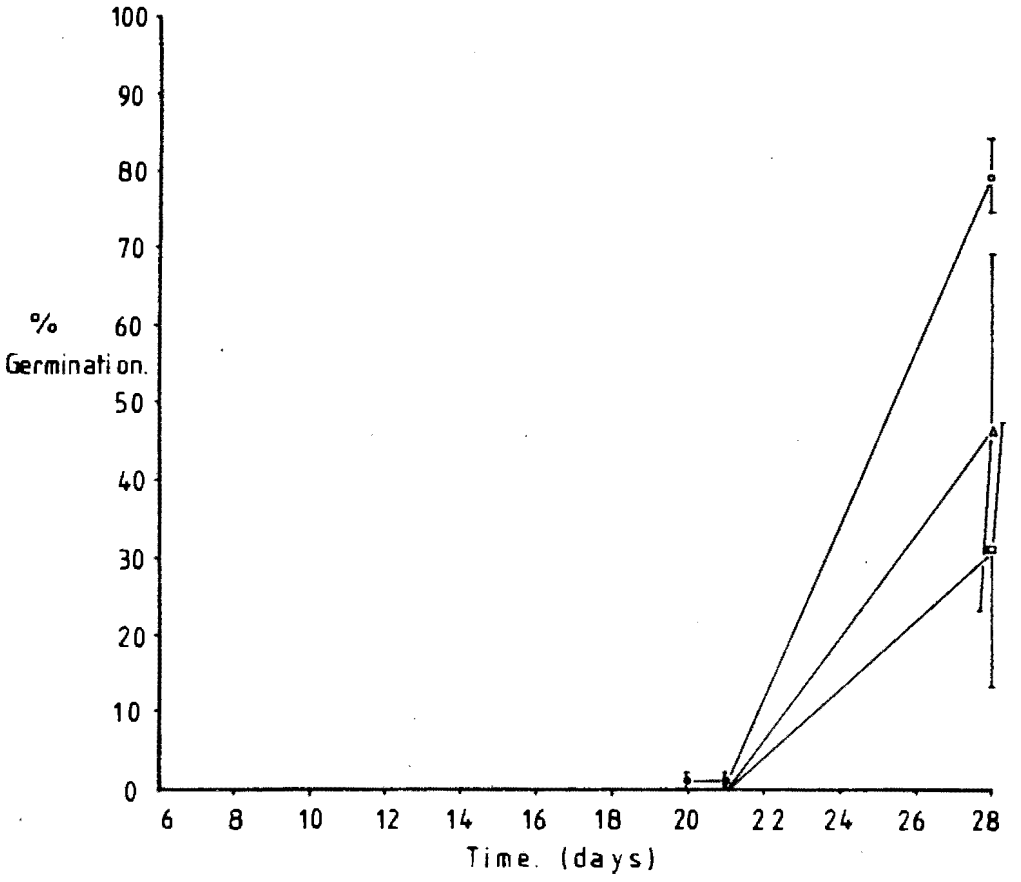


FIGURE 7.21: The germination of fruits from site 2 after exposure to heat in a muffle furnace to simulate the effect of burning. No control is shown here but it would be similar to that shown in Figure 7.4.
The standard error is shown.

- ∘ fruits exposed to 100°C for 60 sec
- ▫ fruits exposed to 200°C for 60 sec
- ▵ fruits exposed to 300°C for 30 sec

atmosphere around the fruits during the burn would probably be higher than that for fruits in direct contact with the burn. Steaming the fruits was used to simulate these conditions.

In Figure 7.22 the germination of fruits from sub-site 2.3 exposed to steam saturated air at 50°C and 60°C for 10 minutes is shown. The control is fruits from sub-site 2.3 that have had no pre-treatment. Fruits from sub-site 2.3, leached for 4 days, were used as a second control. Neither of these two exposures produced any variation from either the untreated control or the leached control. The leached control shows a slightly quicker response to germination but rates and percentage germination were unaltered by steaming the fruits.

In Figure 7.22 only the results of 10 minutes exposure at 50°C in shown. However, the results of exposure for 30 minutes and 60 minutes produced no variation from the above pattern. Figure 7.23 shows the effect of prolonged exposure to steaming at 65°C. Again fruits from sub-site 2.3 were used. No control has been plotted but this control is the same as in Figure 7.22 and is very similar to the 10 and 20 minute exposure in this experiment. The exposure times were 10, 20, 30, 45 and 60 minutes. No enhancement of germination was achieved. The most favourable exposures at 65°C are for 10 and 20 minutes where no apparent damage is caused. At 30 minutes exposure the rate and percentage germination have decreased by about half while after 45 and 60 minutes both rate and percentage germination are very low, below 20% germination after 21 days.

From laboratory experiments it has not been possible to simulate field observations that fire stimulates nassella tussock germination. All the experiments undertaken showed that lower temperatures or shorter exposures used

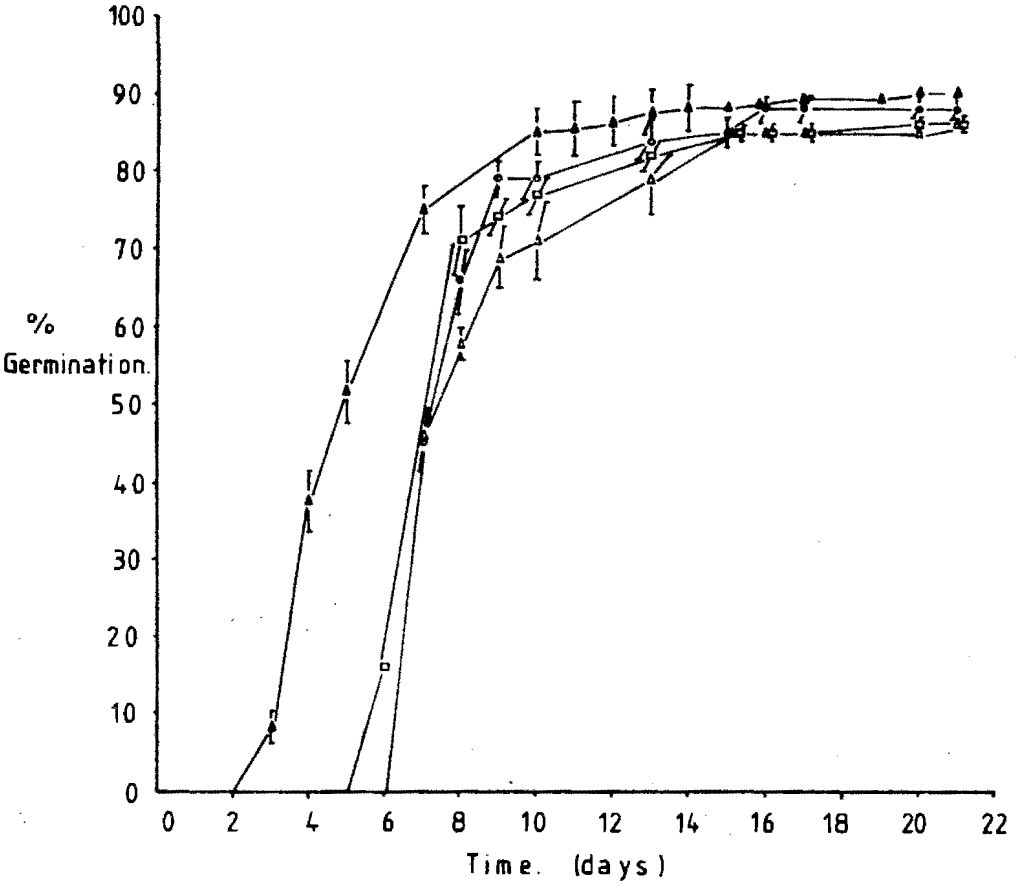


FIGURE 7.22: The germination of fruits from sub-site 2.3 after exposure to steam to simulate the effect of burning on buried fruit. Leached and untreated fruits were used as controls.
The standard error is shown.

- ◦ Control, untreated fruits.
- ▲ Control, fruits leached for 4 days.
- △ Fruits exposed to 50°C for 10 minutes.
- ▫ Fruits exposed to 65°C for 10 minutes.

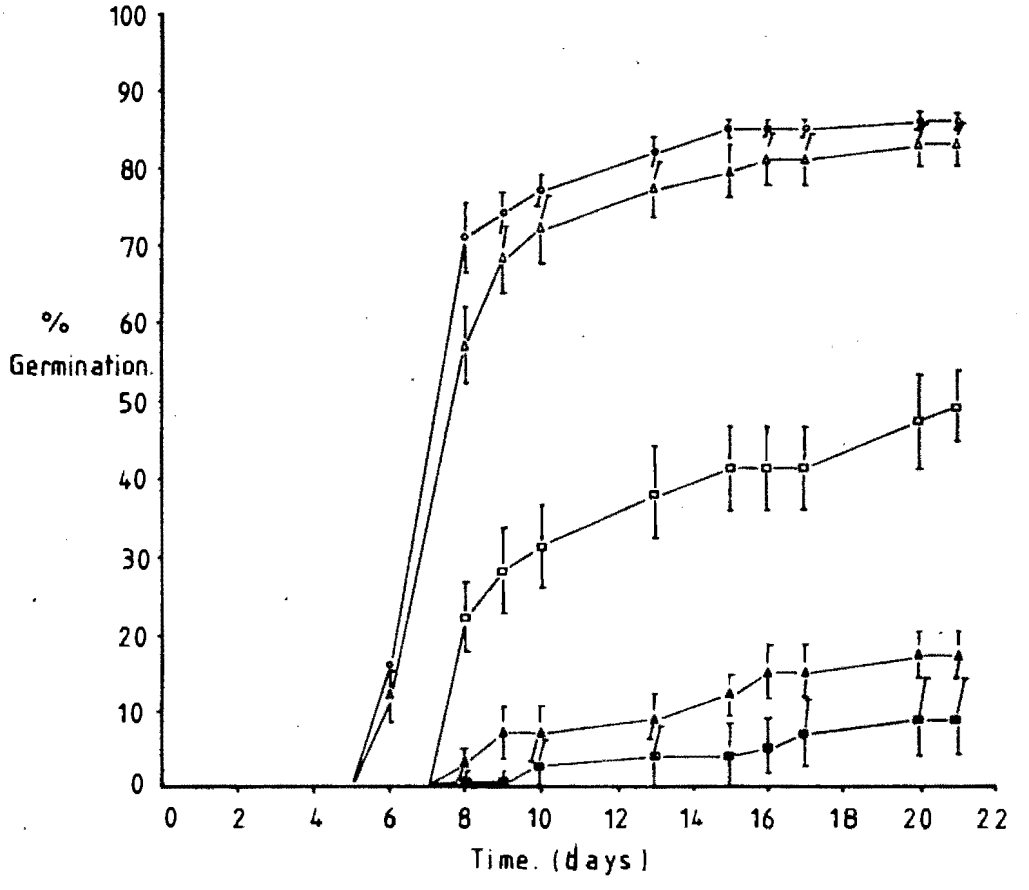


FIGURE 7.23: The germination of fruits from sub-site 2.3 after exposure to steam at 65°C to determine the effect of burning on buried fruit. No control is shown here but both controls in Figure 7.22 can be used. The standard error is shown.

- ▫ Fruits exposed to 65°C for 10 minutes.
- ▵ Fruits exposed to 65°C for 20 minutes.
- ▫ Fruits exposed to 65°C for 30 minutes.
- ▲ Fruits exposed to 65°C for 45 minutes.
- ■ Fruits exposed to 65°C for 60 minutes.

had no effect on the germination. The higher temperatures and longer exposures used appeared to kill or damage the fruits. The observed effect of fire in the field cannot be disputed and therefore must be as a result of an indirect effect of fire on the fruits. The most probable factor in the enhancement by fire would be the removal of competition and thereby allowing the germination of nassella tussock. The removal of or lack of competition is an important factor in the establishment of nassella tussock communities (Healy, 1978) and is not restricted to the effect of burning.

7.7 THE EFFECT OF DIFFERENT SOIL SUBSTRATES ON THE GERMINATION OF NASSELLA TUSSOCK FRUITS

Nassella tussock in the Western Cape is, at present, mainly found on soils derived from the Malmesbury shale formation. The Banhoek infestation is found on a soil with a similar colour and physical composition (see Section 3, Distribution). Healy (1978) states that the Cape Flats appears to be an ideal area for the establishment of nassella tussock. However, there is no record of nassella tussock on the Flats although it appears to have been known to be on Rhodes Estate for about 40 years (Hall & Bulley, 1980). This suggests that a factor or complex of factors is operative in limiting or preventing the establishment of nassella tussock on the Cape Flats. The major differences between the Cape Flats and Rhodes Estate are the soil, rainfall and vegetation. The rainfall decreases with an increase in distance from Table Mountain (Moll and Campbell, 1976). However, nassella tussock is adapted to arid areas (Wells, 1974) and should, therefore, not be affected by the lower rainfall of the Cape Flats.

The vegetation of the Flats is mostly exotic Acacia species which have developed into dense stands. However, clearing

operations for roads or for firewood leave large areas of disturbed ground where nassella tussock should be capable of invading. The soil of the Flats is a coarse, white sand, markedly different to the fine brown soil of Rhodes Estate. Although Healy (1945) stated that nassella tussock infestations are not limited by soil differences, it was felt that the substrate differences between the two sites in question could be responsible for the pattern of distribution.

7.7.1 Germination on Rhodes Estate Soil versus Cape Flats Sand

Fruits from sub-site 2.3 which had been leached for 5 days were placed about 2,5 mm below the surface of both 2,0 mm sifted Rhodes Estate soil and Cape Flats sand. Leached fruits on filter paper were used as a control.

Fruits buried in the soils showed a lower germination rate than that of the control (Figure 7.24). The control shows the usual pattern of rapid germination in the first 10 days, with a maximum of 90% after 21 days. Fruits placed in the Rhodes Estate soil started to germinate on the 7th day while those in the Cape Flats sand started on the 9th day. The germination of the fruits in the Rhodes Estate soil remained insignificantly higher than that in the Cape Flats sand until the 12th day. From this point the rate of germination increased in the Cape Flats sand until on the 21st day the percentage germination in the Cape Flats sand was midway between the control and the Rhodes Estate soil germination.

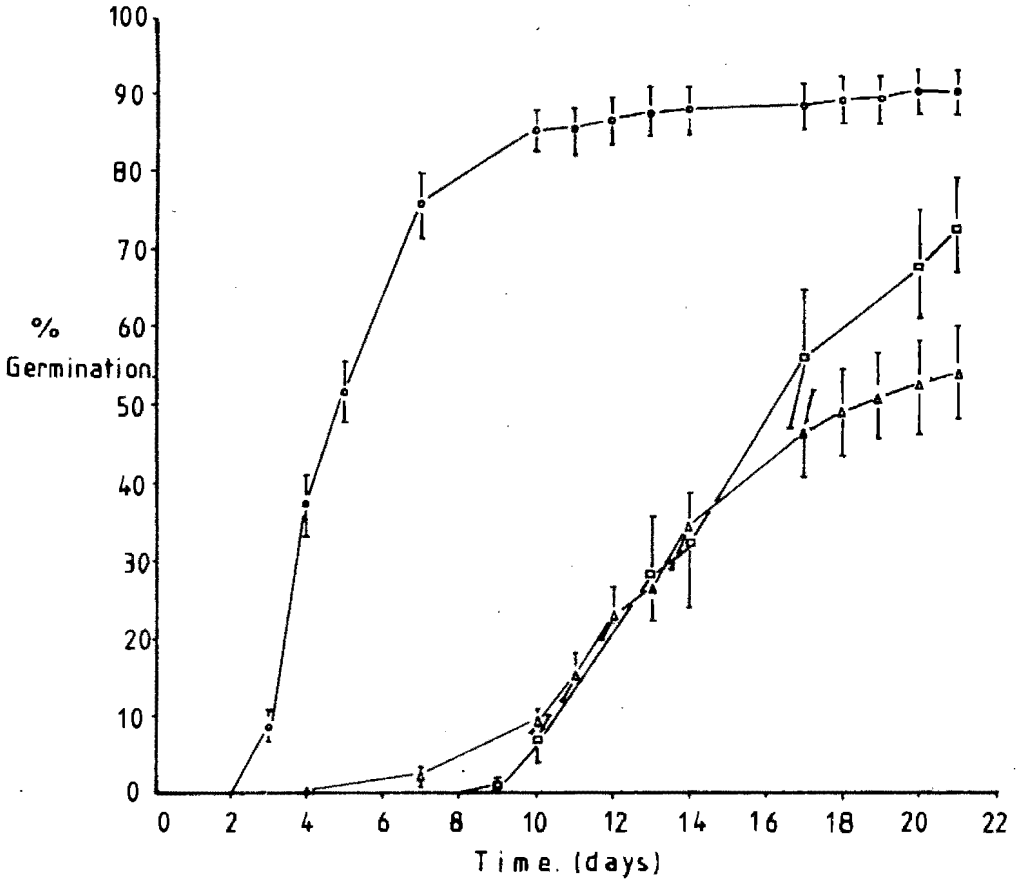


FIGURE 7.24: The germination of fruits from sub-site 2.3 buried in 2,5 mm of Rhodes Estate soil and Cape Flats sand. All the fruits were first leached for 5 days. Fruits germinated on filter paper served as a control.
The standard error is shown.

- ◦ Control
- ▵ Fruits buried in 2,5 mm Rhodes Estate soil
- ▫ Fruits buried in 2,5 mm Cape Flats sand.

The experiment was repeated using fruit, leached for 5 days, from Thomas River, Eastern Cape. The results are expressed in Figure 7.25 and show the same pattern as that obtained with the fruits from sub-site 2.3. These results show that fruit from the Western Cape and Eastern Cape is capable of germinating on both Rhodes Estate and Cape Flats soil. However, the presence of both soils resulted in a larger decrease in the final percentage germination and in considerably lower rates of germination. The main point in question is how the germination on the two soils compare with each other, not the control. In both Figure 7.24 and 7.25 it is clear that the difference in rate and percentage germination on the two soils is small although the Cape Flats soil results in higher levels of germination.

These results coincide with Healy's (1945) statement of there being no preference for any particular soil. The results show that nassella tussock would germinate more rapidly on Cape Flats soil and could, therefore, be expected to be more common on the Cape Flats. This is, however, over simplified as rate of establishment and the effect of competition have not been considered.

7.7.2 The Effect of the Depth of Burial on the Germination

Fruits from sub-site 2.3 were buried in various depths of Rhodes Estate soil and Cape Flats sand to determine whether that part of the seed store that is buried in the field is readily available for germination. Fruits, leached for 4 days, were placed on the surface of both soils as control and buried at 10, 20, 30 and 40 mm below the surface.

Those fruits placed in Rhodes Estate soil, except for the fruits on the surface, produced no germination. Germination

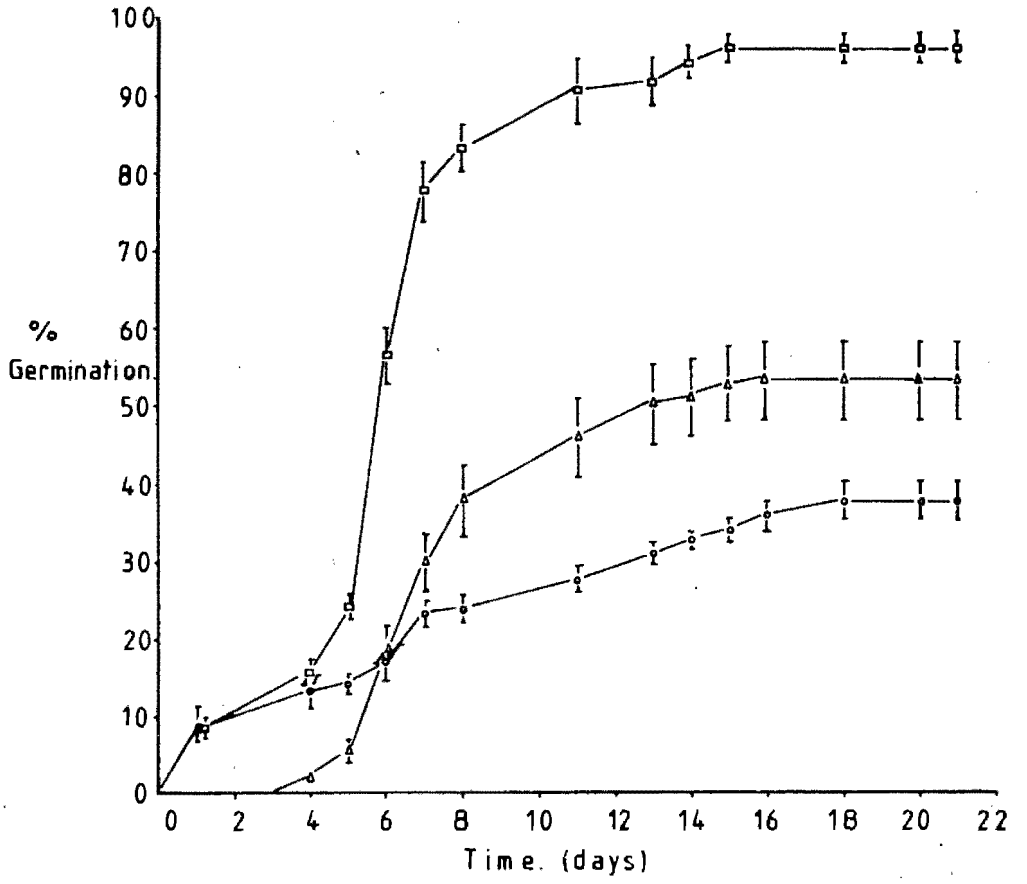


FIGURE 7.25: The germination of fruits from Thomas River buried in 2,5 mm Rhodes Estate soil and Cape Flats sand. All fruits were first leached for 5 days. Leached fruits germinated on filter paper served as a control.
The standard error is shown.

▫ Control

▵ Fruits buried in 2,5 mm Cape Flats sand.

◦ Fruits buried in 2,5 mm Rhodes Estate soil.

of the fruits placed on the surface was rapid and very similar to that that had been achieved on filter paper (Figure 7.26). All the fruits in the buried samples failed to germinate. If the germination of the fruits buried at 2,5 mm, in Section 7.7.1, is compared it can be seen that this covering of only 2,5 mm produced a marked decrease in the germination (cf. Figure 7.24).

The situation with Cape Flats sand is markedly different from that described above. Germination of the fruits on the soil surface was high, at 96%. This was only marginally higher than that achieved on the Rhodes Estate soil (92%) (Figure 7.26). The fruits bruied at 10 mm started to germinate after 8 days while those at 20 mm started after 17 days. No germination was recorded at 30 and 40 mm, even after 35 days. The final percentage germination at 10 mm was low, producing only 28% after 21 days. Not shown in Figure 7.26 is that although the curve is in the acceleration phase, the final percentage germination achieved at 10 mm was 30% after 35 days. At 20 mm only 4% germination was achieved. If the results of Section 7.7.1 are used in conjunction with these results (cf. Figure 7.24 and 7.26) it can be seen that burial at 2,5 mm produced a significant decline in the germination. The decline in germination produced by increasing the depth to 10 mm is approximately equal to that achieved by 2,5 mm, that is, approximately half.

Fruits buried in Rhodes Estate soil are unlikely to germinate while those in Cape Flats sand have a greater chance to germinate. This could be caused by a number of factors that could include gas availability, moisture, nutrients and light. The moisture, under experimental conditions, was not a factor as both soils were maintained at near saturation point. Gaseous oxygen is unlikely to have differed markedly as both soils were treated identically. Nutrients should only play a role after the fruits have

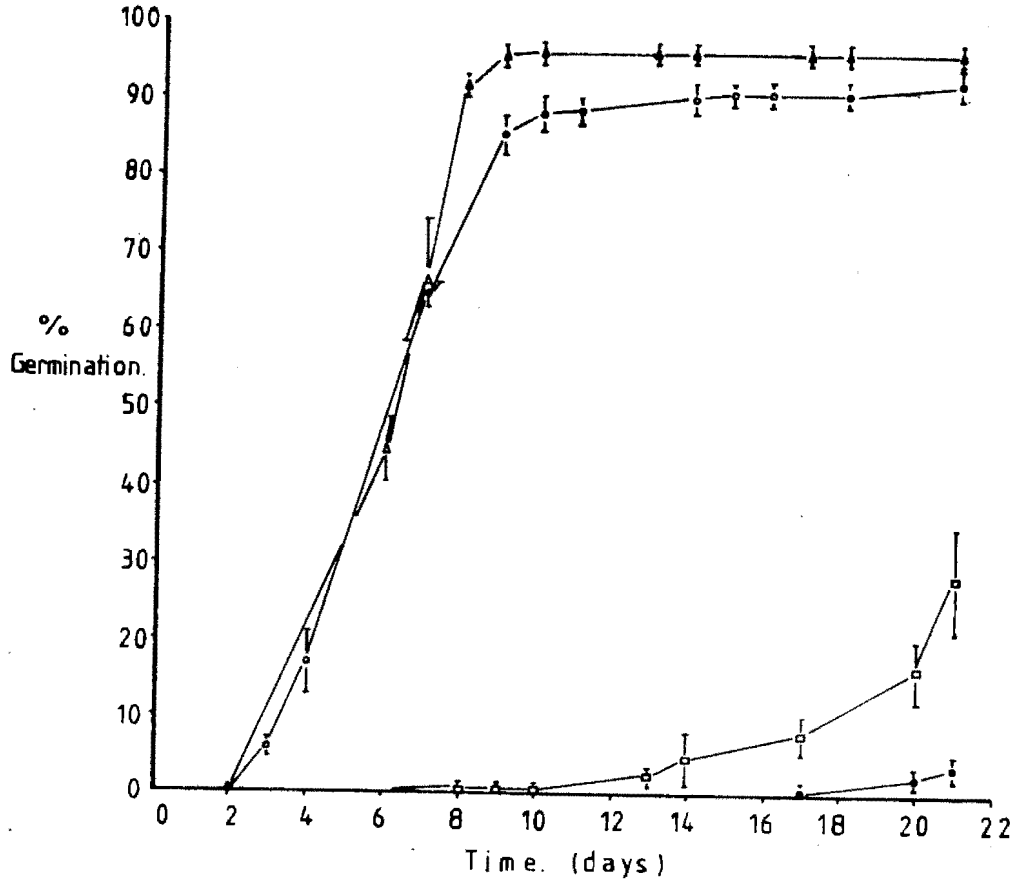


FIGURE 7.26: The germination of fruits from site 2 buried at various depths in Cape Flats sand and on the surface of Rhodes Estate soil. All fruits were first leached for 4 days.
The standard error is shown.

- ∘ Fruits on the surface of Rhodes Estate soil.
- ▵ Fruits on the surface of Cape Flats sand.
- ▫ Fruits buried in 10 mm Cape Flats sand.
- • Fruits buried in 20 mm Cape Flats sand.

germinated, therefore it is possible that light is the limiting factor. The difference in colour and particle sizes of the soils could be a factor in allowing greater light penetration in the Cape Flats sand. The Cape Flats sand is white with large particles while the Rhodes Estate soil is dark with small particles and would, therefore, admit less light than the Cape Flats sand.

7.8 THE GERMINATION OF FRUITS IN THE DARK

Due to limited germination chamber space, not all the probable factors contributing to reduced germination of buried fruits could be tested. Of the probable factors, gas, moisture, nutrients and light, it was felt that light was the most likely cause of the reduced germination. Fruits were placed in petri dishes and then placed in a sealed dark box. This was then placed in the germination chamber. No safe light facilities were readily available for counting the germinating fruits so only a final count on the 21st day was carried out.

The general trend was for most samples to have lower germination in the dark than in the light. The results of unleached fruits of sub-sites 2.1, 2.2 and 1.3 are shown in Figure 7.27. In all three samples there is a significant difference, in the percent germination after 21 days, between light and dark germinated fruits. This reinforces the hypothesis that reduced germination in buried fruits is caused by a reduction in light availability.

The experiment was repeated, using leached fruits in the dark and both leached and unleached fruits as light controls. The results, expressed in histogram form, showing the percent germination after 21 days for each sub-site, are shown in Figur 7.28. The first column represents the dark germination, the second the leached control and the

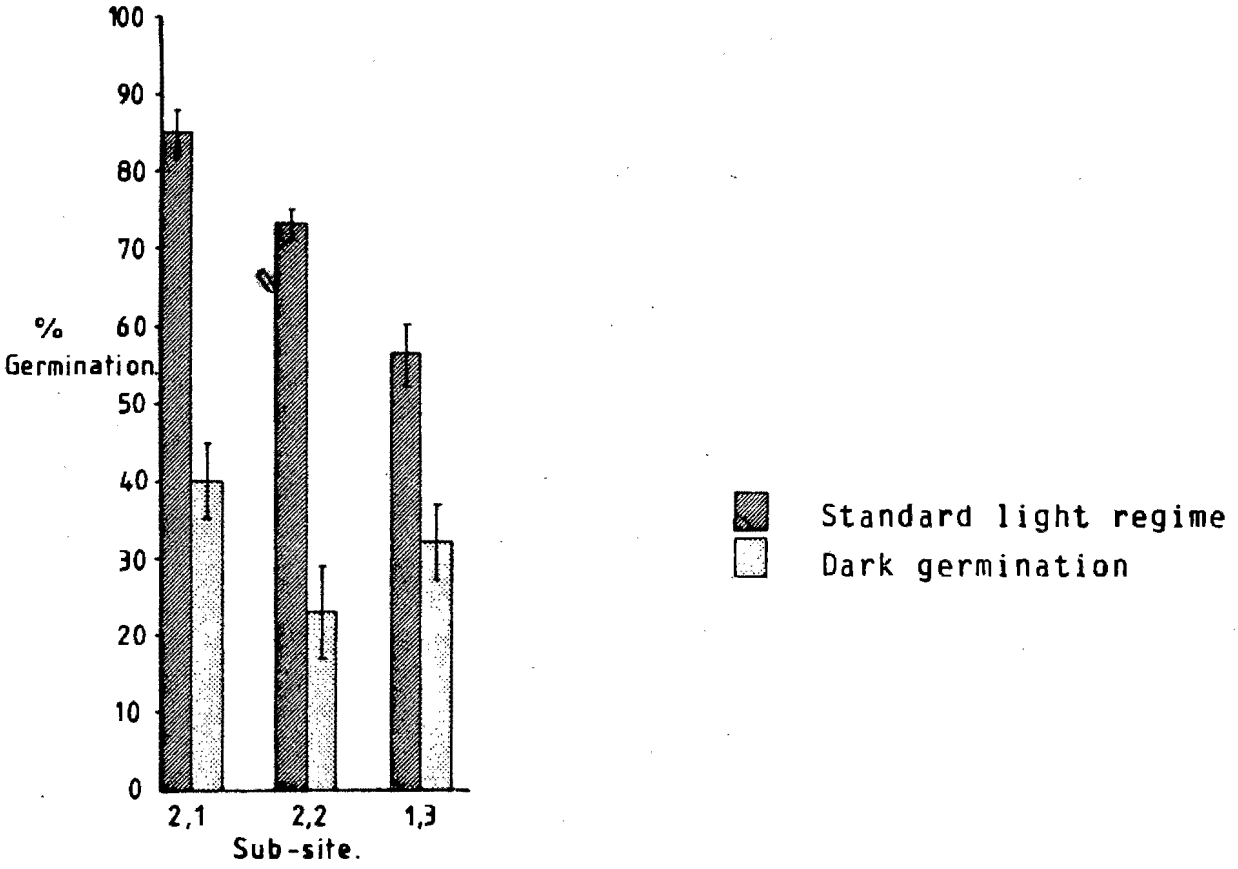
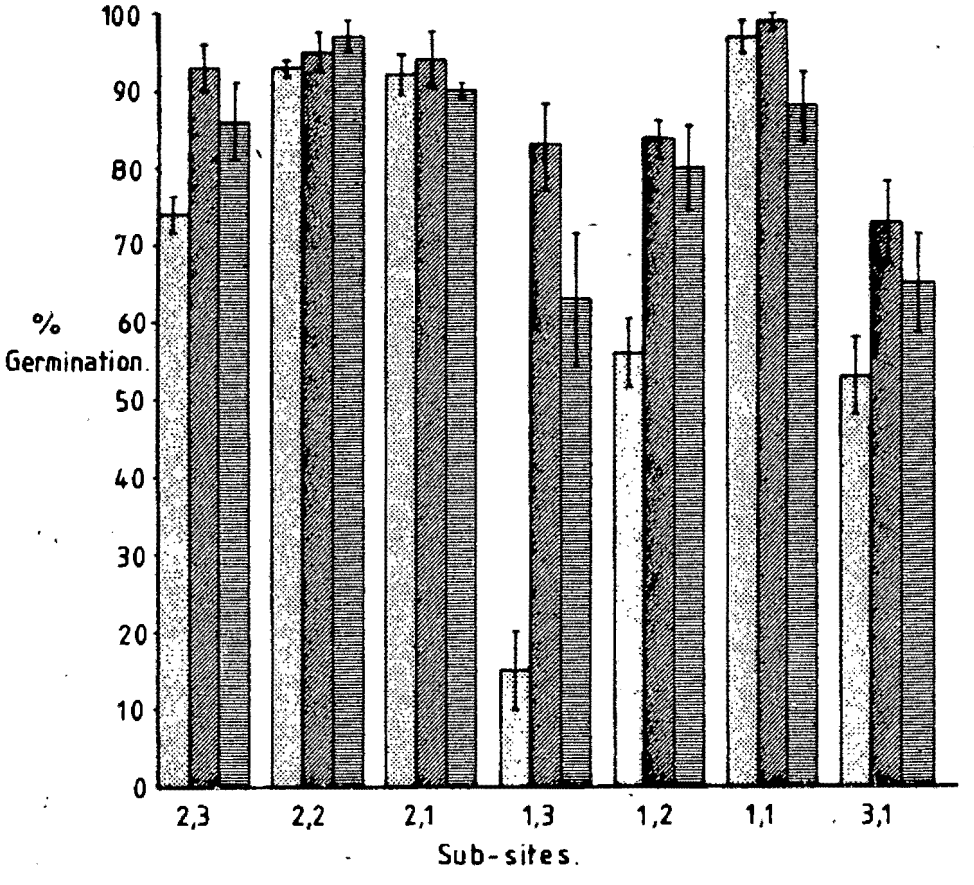


FIGURE 7.27: The germination of untreated fruits of site 2 after 21 days in total dark and the standard light regime.
The standard error is shown.



Dark germination, leached for 4 days
Standard light regime, leached for 4 days
Standard light regime, untreated.

FIGURE 7.28: The germination of leached fruits of sites 1 and 2 and sub-site 3.1 in the dark and under the standard light regime, after 21 days. An untreated sample of fruits of each was also germinated under the standard light regime.
The standard error is shown.

third, the unleached control. In sub-sites 2.2, 2.1 and 1.1 there is no significant differnece between dark and light germination. In these three sub-sites the light, leached control is always higher than the dark germination but the untreated control in sub-sites 2.1 and 1.1 is lower than the dark germination. Sub-sites 1.3 and 1.2 show the largest reduction of germination by the dark treatment. In sub-sites 2.3 and 3.1 the dark germination is also lower than both controls but he differences are not very great.

These results contradict the first experiment carried out with germinating fruits in the dark. They show that in some cases the fruits germinate poorly in the dark while others, from other sub-sites, germinate readily in the absence of light. This highlights differences noted before that it is difficult to make generalizations about nassella tussock on Rhodes Estate as it appears to respond differently from one sub-site to the next.

7.9 THE GERMINATION OF NASSELA TUSSOCK IN RELATION TO FRUIT AGE

Nassella tussock fruits are reported to remain viable in the soil for many years, possibly as many as 20 (Healy, 1945, Wells, 1974). If the fruits do remain viable for long periods it would be interesting to know what the changes in the germination pattern would be. Unfortunately this is a long term project and could not be incorporated in the present work. However, fruits from two seasons, 1980 and 1981, were compared to determine whether there was any change in the germination pattern.

Fruits from sub-sites 1.3, 2.3 and 3.1, from both the 1980 and 1981 flowering seasons, were leached for 4 days and then subjected to the standard germination procedures (Section 2.4.1).

The same pattern emerged for the three sub-sites used in this experiment. The 1981 fruits started to germinate first while the 1980 fruits showed delayed germination (Figures 7.29, 7.30 and 7.31). In the case of sub-site 2.3 (Figure 7.29) the 1980 fruits had a slow initial phase of germination which has not appeared before while using fruits from the current year. However, the rate of germination increased on the 5th day and the 1980 fruits ended with a higher percentage germination than the 1981 fruits.

With the fruits from sub-site 1.3, the delay before the 1980 fruits started to germinate was much more marked, with germination only starting after 7 days. In the 1981 sample, germination was recorded on the first day (Figure 7.30). As with sub-site 2.3 the 1980 fruits produced a higher final percentage germination than the 1981 fruits.

The pattern with fruits from sub-site 3.1 was similar to that of sub-site 2.3. The delay in germination was minimal with there being no significant difference between the two seasons' fruits after 3 days. However, after 21 days, the 1980 fruits had produced 95% germination while the 1981 fruits produced only 65% (Figure 7.31). This difference in final percentage germination was also the major difference found between sub-site 3.1 and sub-sites 1.3 and 2.3 (cf. Figures 7.29, 7.30 and 7.31).

The results show that ageing by one year causes little change to the germinability of the fruits. Ageing could be expected to have one of two effects on fruits. Firstly, it could cause a decrease in the germination of the fruits due to senescence of the embryo. Secondly, ageing could enhance the germination via an after-ripening effect either in the embryo or by the change in structure of the lemma and palea, thereby making it more permeable to gases and less restrictive as a mechanical barrier. A further after-ripening effect could be the decrease in amount of inhibitor in the fruit.

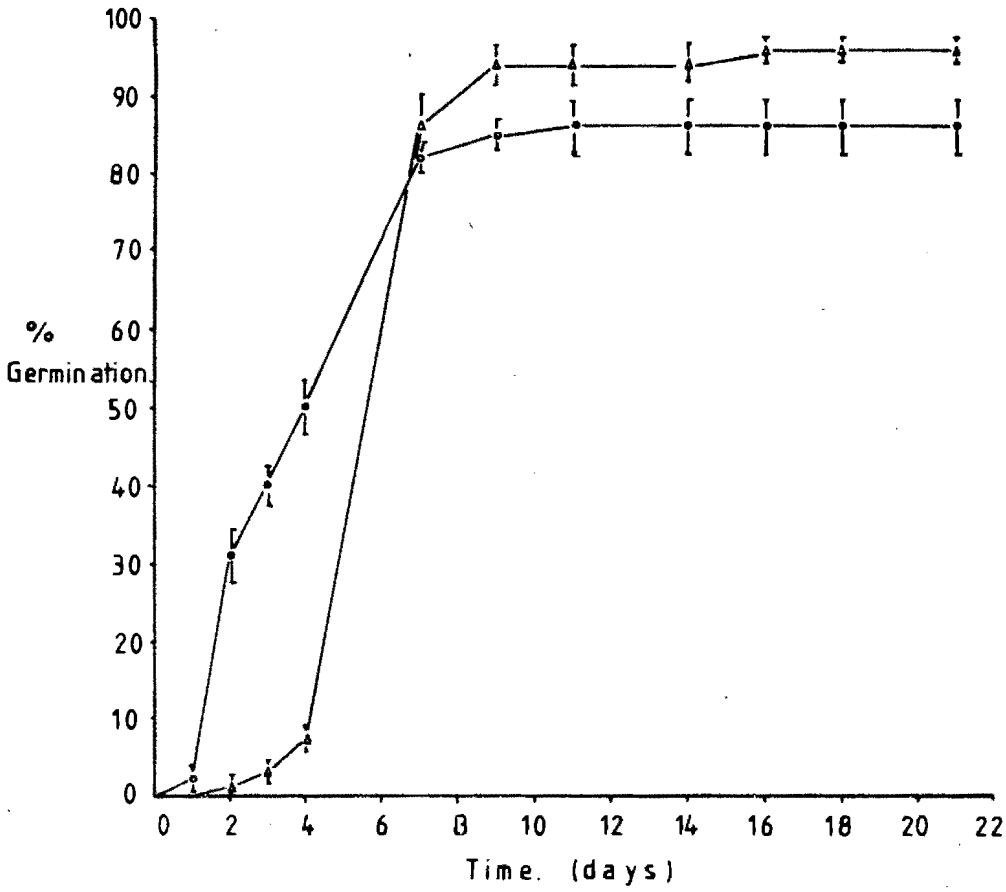


FIGURE 7.29: The germination of fruits from sub-site 2.3 from the 1980 and 1981 flowering seasons. The fruits were leached for 4 days.
The standard error is shown.

∘ Fruits from 1981

▵ Fruits from 1980.

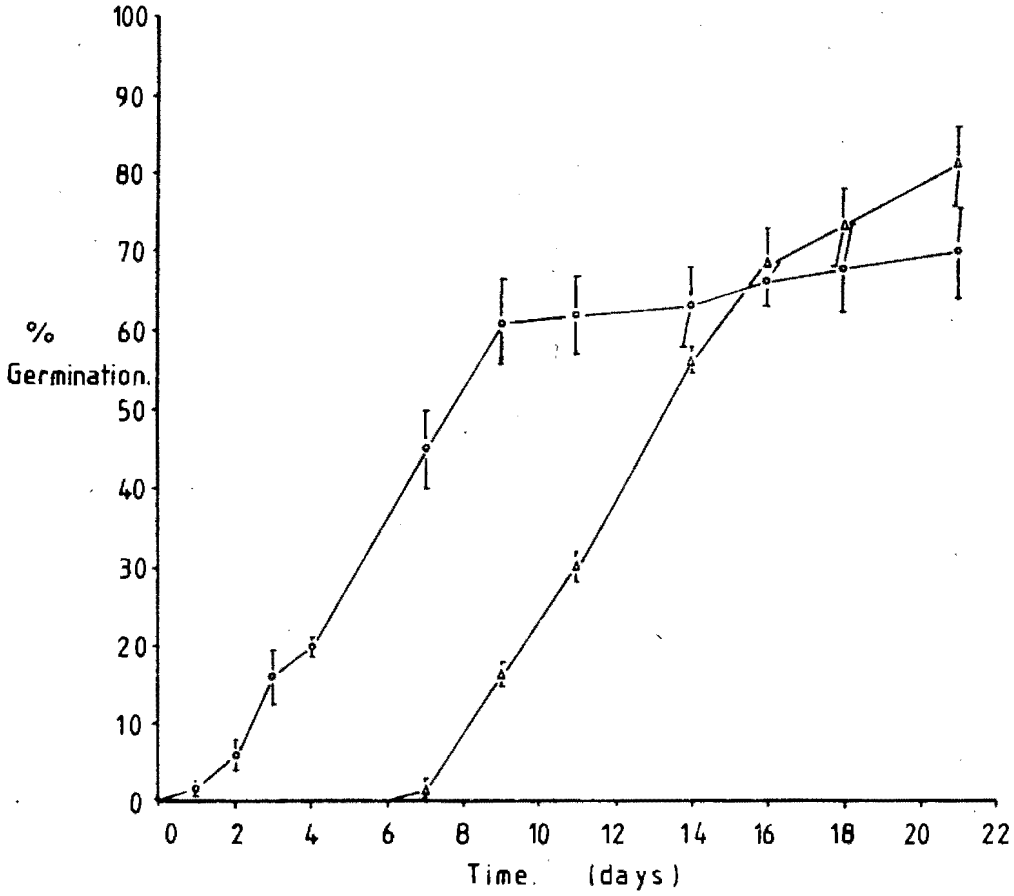


FIGURE 7.30: The germination of fruits from sub-site 1.3 from the 1980 and 1981 flowering seasons. The fruits were leached for 4 days.
The standard error is shown.

∘ Fruits from 1981

▵ Fruits from 1980.

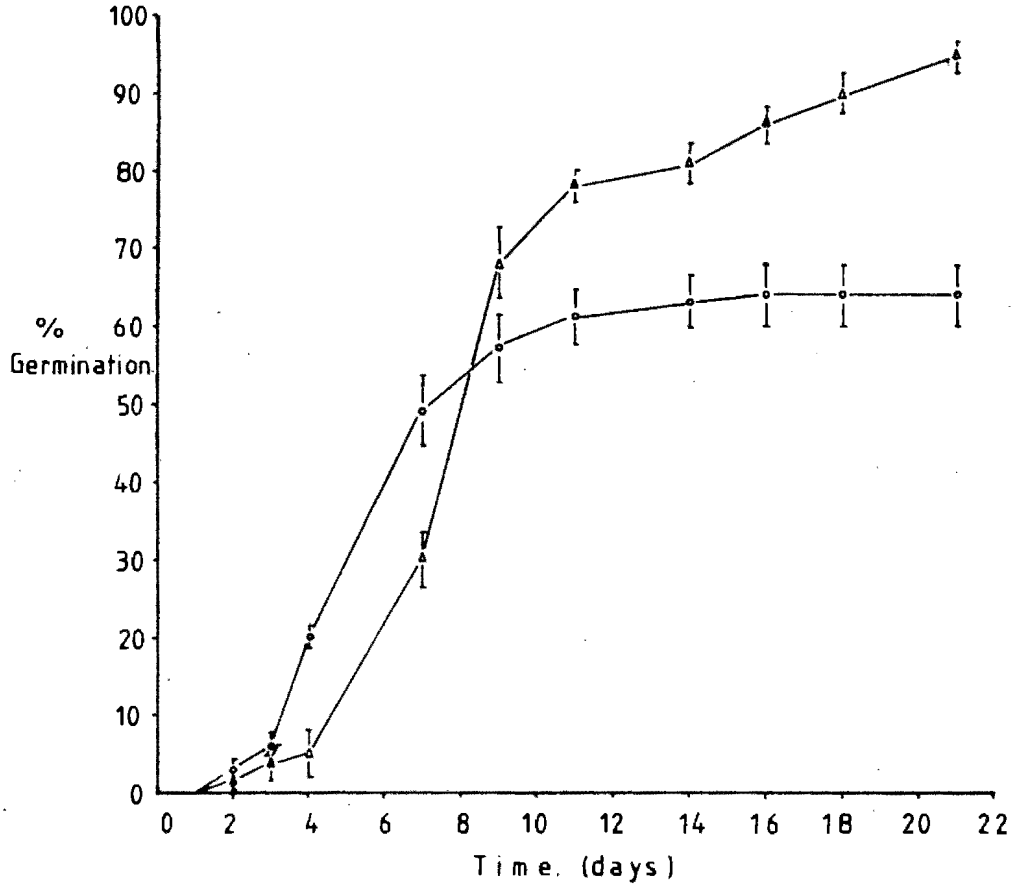


FIGURE 7.31: The germination of fruits from sub-site sub-site 3.1 from the 1980 and 1981 flowering seasons. The fruits were leached for 4 days.
The standard error is shown.

∘ Fruits from 1981

▵ Fruits from 1980.

The results from this experiment initially support that ageing has a negative effect on the germination of nassella tussock by causing various degrees of decreased rate of germination in the initial days. However, the subsequent increase in rate and the higher final percentage germination of fruits of 1980 contradicts any adverse effect of ageing. This increase in germination supports that ageing is preferable for nassella tussock germination. The cause of the decreased initial rate and increased final germination could be any of a number of factors. These were not investigated in this study. The increase in germination could, however, be as a result of a decrease in inhibitors in the fruit. This corresponds to work done on the leaching of inhibitors (Section 7.3.1 and 7.5) which showed that an inhibitor or complex of inhibitors were probably being removed from the lemma and palea.

7.10 THE VARIATION OF FRUIT SHAPE AND COLOUR AND ITS POSSIBLE EFFECT ON GERMINATION

7.10.1 Shape Variation

Variations in fruit shape were discussed under Phenology (Section 6.4). It was suggested that tussocks growing in strong sunlight had florets that opened for fertilization and produced long, thin fruits. Florets from shaded tussocks or shaded areas of a tussock remained closed, that is, they appear to be self-pollinated and produce short, round fruits. In this section the germination performance of these two fruits types is investigated.

Fruits from sub-site 1.3 were used. These were first separated into the two size categories, leached for four days and then subjected to the standard germination procedures

(Section 2.4.1). An unsorted sample from sub-site 1.3 was used as a control. The results of this experiment are shown in Figure 7.32. From this it can be seen that the shape of the fruit or the method of fertilization does affect the germination but this effect is minimal. The two shapes show very similar levels of germination up to the 13th day. From this point the long fruits show a higher rate of germination up to the 16th day when the rate of the round fruits increases. The final percentage germination of both varieties, at 21 days is similar with the long fruits at 88% and the round fruits at 80%. The germination of the control, mixed sample was similar to the round fruits only until the 16th day. The final percentage germination of the control was 55% after 21 days. This was surprising as a control made up of a mixed sample would have been expected to have had a germination pattern midway between the two shape variants.

7.10.2 Colour Variation

Apart from shape variation, a variation of fruit colour within samples was also noted. Nassella tussock fruits are generally described as being light brown (Healy, 1945). This was seen to be the general colour of most samples but could differ from white to dark brown, almost black. The white fruits are generally all non-viable and consist of 'empty' lemmas and paleas. These white fruits are easily squashed between one's fingers. The next stage in the colour range is a light brown fruit, which is typically hard, is difficult to squash and is viable. The dark fruit is also hard, difficult to crush and viable but is dark brown to grey-black in colour. The occurrence of these colour variations differed within and between samples. In all the samples from Rhodes Estate the fruits were found to cover the whole colour spectrum just described, and not to favour either of the extremes, that

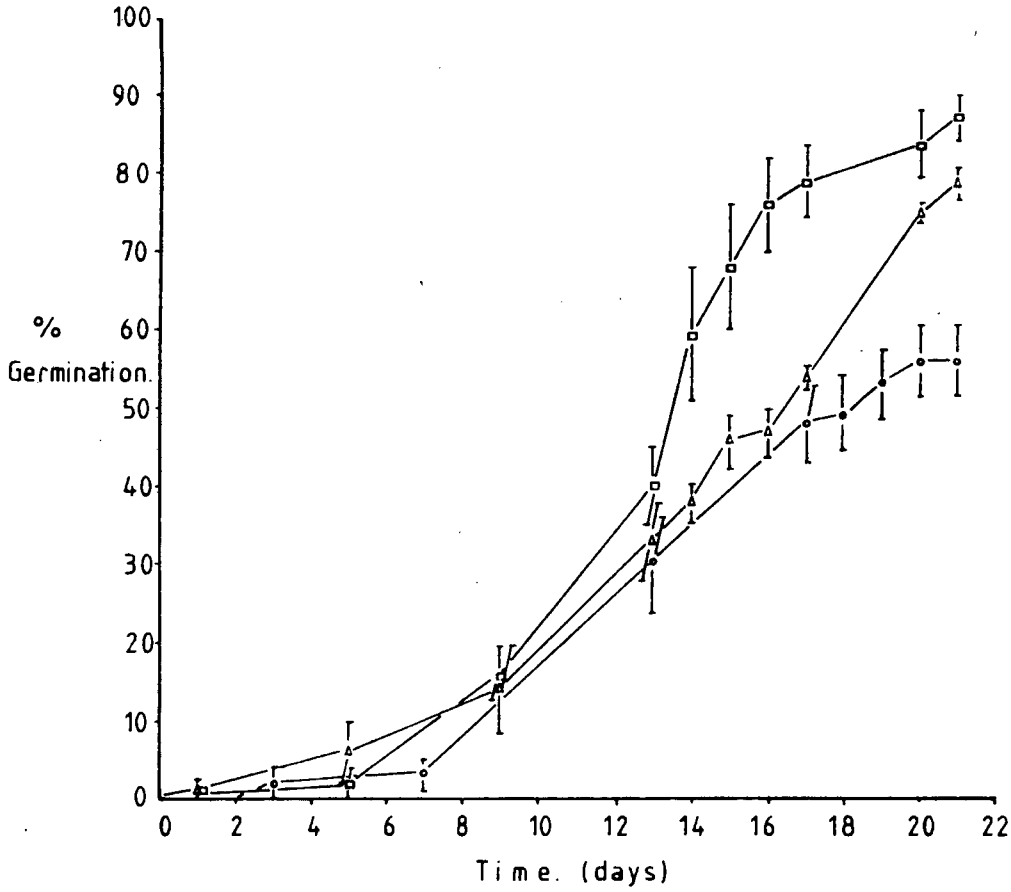


FIGURE 7.32: The germination performance of different fruit shapes from sub-site 1.3.
All fruits were leached for 4 days.
The standard error is shown.

Unsorted sample, control

Short round fruits.

Long thin fruits.

is, either the light or dark variants. Insufficient numbers of the extremes were available to allow for germination trials on the colour variants.

The sample from Thomas River, Eastern Cape, fruits that had been used in previous experiments was found to have the same colour variants. However, the number of extreme colours was greater so these fruits were used in a germination trial as described in Section 2.4.1. All fruits used were first leached for 5 days (Section 2.4.2). The results are shown in Figure 7.33. The light fruits show a high rate of germination, reaching a peak of 96% in 15 days. The dark fruits have a much lower rate and percentage germination, reaching only 50% after 21 days. The control, made up of an unsorted fruit sameple, is roughly midway between the two colour extremes (Figure 7.33). The germination of the light fruits is more uniform than the dark fruits. This is seen in Figure 7.33 by the smaller standard errors of the light fruits.

7.11 THE EFFECT OF EXPOSURE IN THE FIELD ON GERMINATION

This experiment was aimed at determining whether fruits in the field remained viable or not. It was proposed to determine the viability of fruits buried at 40 mm and fruits exposed on the soil surface for various lengths of time. The fruits used in the experiment had been collected from Rhodes Estate during 1979 and had been found to have a firly low germination rate and percentage (about 65% after 21 days).

Fruits exposed for 2, 4, 6 and 8 months were subjected to the standard germination procedures (Section 2.4.1). In Figure 7.34 the results of fruits exposed on the soil surface are shown. No statistical analysis was done as insufficient replicas were available after fruit loss in the field. Only about 60% of the fruits placed in the

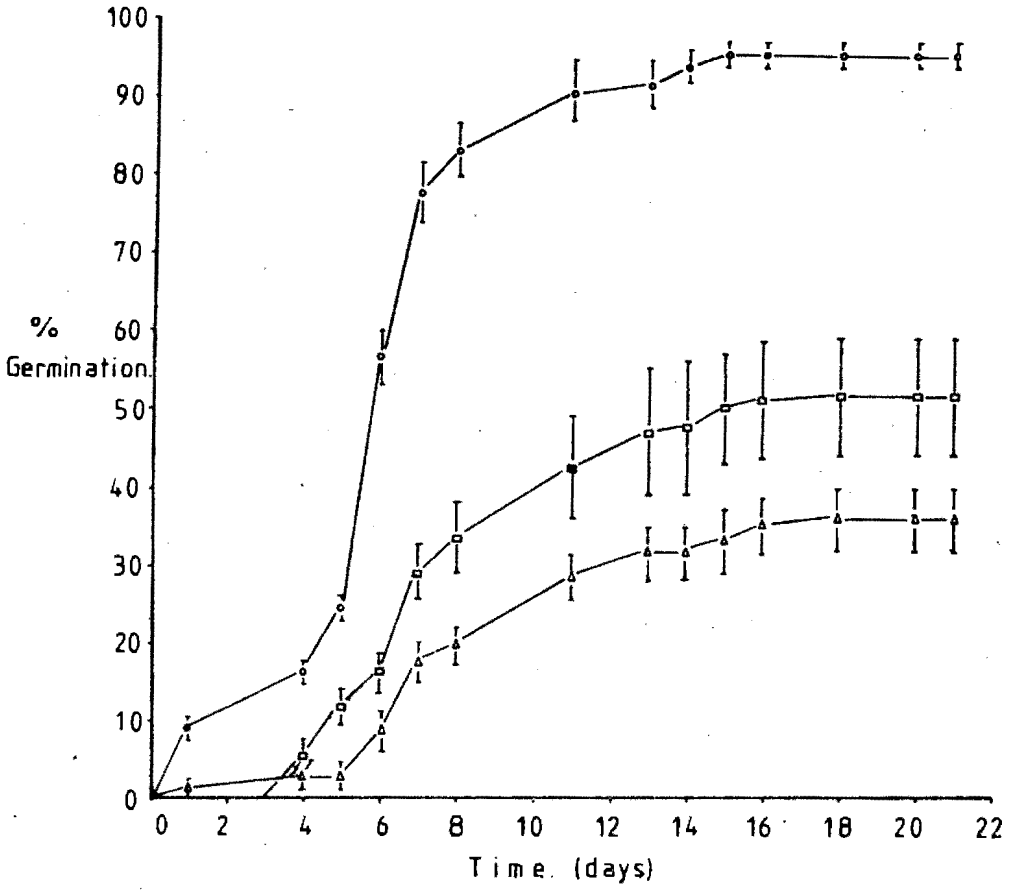


FIGURE 7.33: The germination performance of different fruit colours from Thomas River.
All fruits were leached for 5 days.
The standard error is shown.

▫ Unsorted sample, control

◦ Light round fruits.

▵ Dark round fruits.

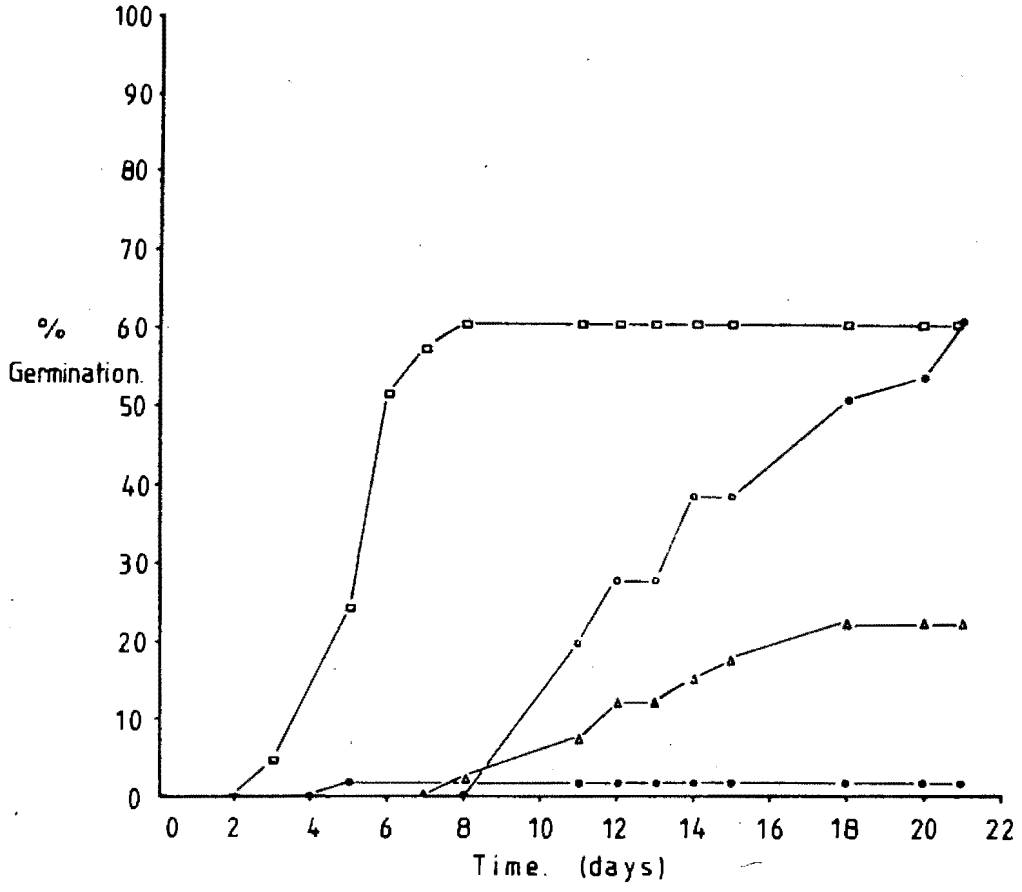


FIGURE 7.34: The germination of fruits exposed on the soil surface of Rhodes Estate for various periods of time. No pre-treatment was applied. No statistical data are available.

- ◦ 2 months exposure
- ▲ 4 months exposure
- ▫ 6 months exposure
- • 8 months exposure

field on the 26 June 1980 were retrieved. The results obtained were unexpected because after 2 months exposure the fruits displayed an 8 day delay followed by a high rate of germination with a final level of 60% after 21 days. For the fruits exposed for 4 months the delay was only 2 days. This was followed by rapid germination, reaching 60% after 8 days and then having no further germination. After 6 months' exposure the rate and percentage germination were both lower. The fruits exposed for 8 months showed very low germination, reaching 2% after 5 days and not germinating for the rest of the experiment. This decrease in germination with the increase in the length of exposure as seen from 4 months through to 8 months exposure is the pattern that would be expected. This would most probably be as a result of decay of the fruits by both weathering and microbial action. However, the extent of the reduction in germination is questionable as these limited results suggest that after only 8 months' exposure only 2% germination is achieved. This points to a very low survival rate of surface exposed fruits.

The results for fruits buried at approximately 40 mm, on the 26 June 1980, are shown in Figure 7.35. The pattern seen here is for an increase in germination and a decrease in the time to germination with the increased burial times. The only exception is seen where the 2 months' burial has a higher final percentage germination than the 4 months' burial. However, the 2 month burial fruits do have a longer time to germination than the fruits buried for 4 months. These results suggest a positive effect of shelter by burial of fruits. This could either be caused by an ageing of the embryo, leaching of inhibitors or decay of the lemma and palea. The physical appearance of the lemma and palea tend to discount the possibility of decay of these structures causing the enhancement of germination (see Chapter 9). The results shown with fruits of 1980 and 1981 (Section 7.9) suggest that ageing

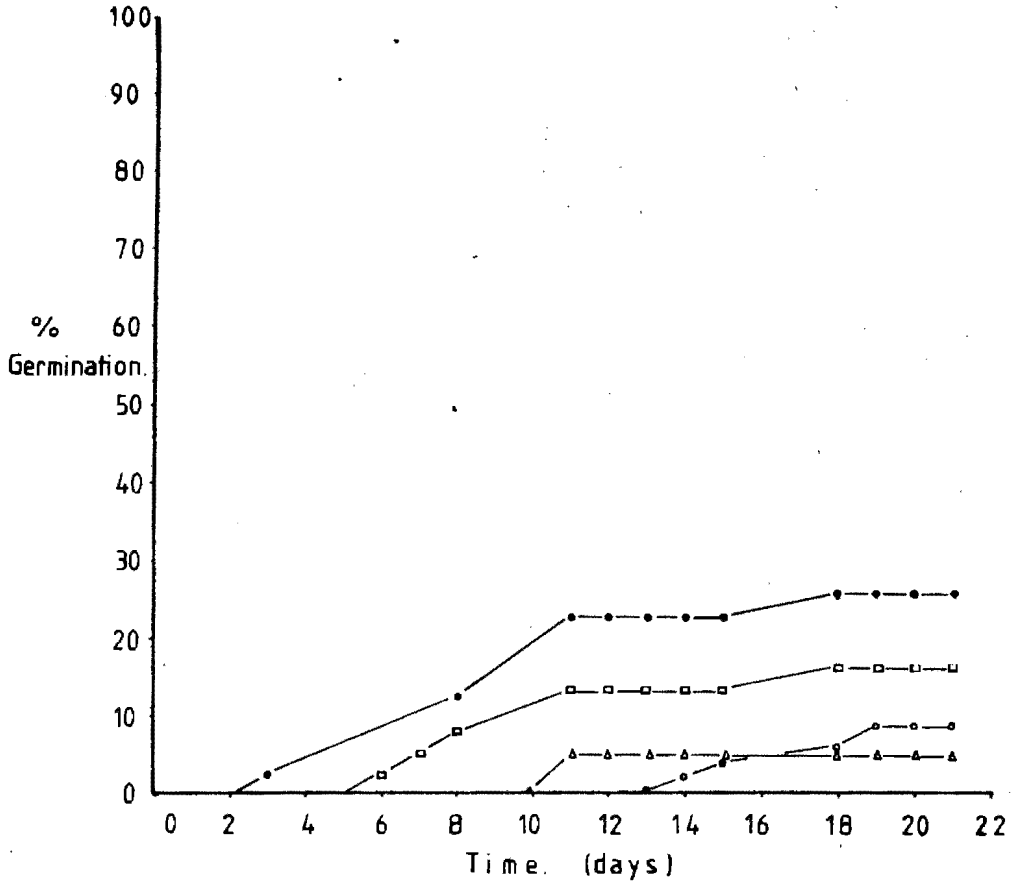


FIGURE 7.35: The germination of fruits buried at approximately 40 mm on Rhodes Estate for various periods of time. No pre-treatment was applied. No statistical data are available.

- ◦ 2 months burial
- ▵ 4 months burial
- ▫ 6 months burial
- • 8 months burial

does not manifest itself in this gradual increase in percentage germination and decrease in time to germination. It would appear, therefore, that the probable cause is either a decrease in inhibitor action or the leaching of an inhibitor or complex of inhibitors from the fruit (cf. Section 7.3, leaching).

7.12 GERMINATION OF NASSELLA TUSSOCK FRUITS IN THE FIELD

These results are closely related to the results discussed in Section 7.11 While the results in Section 7.11 deal with the germination of fruits after recovery from periods of exposure or burial in the field, these results show the percentage of fruits that apparently germinated while exposed or buried in the field.

The results shown in Figure 7.36 express germination as a percentage of the number of fruits recovered. Recovery of buried fruits was consistently high with a recovery rate always above 75% (Figure 7.36). The germination of buried fruits in the field was low after 2 and 4 months. It then declined to 2% after 8 months with a slight increse after 10 months. This is followed by a further decrease after 12 months. A large increase in germination, after 14 months, is followed by a sharp decrease to 1% after 17 months (Figure 7.36). These results are shown in Table 7.1 where the percentage germination is compared with the season of retrieval and the rainfall for the month of retrieval. For the detailed rainfall pattern see Figure 8.5. From Table 7.1 it can be seen that the highest germination was recorded in late winter (August 1980 and 1981) to spring (October 1980). The summer germination varies from 25% to 1% while the winter germination was recorded at 5%. Autumn germination (April 1981) at 15% was also relatively low. From these results there appears to be no apparent connection between rainfall and percentage germination on Rhodes Estate.

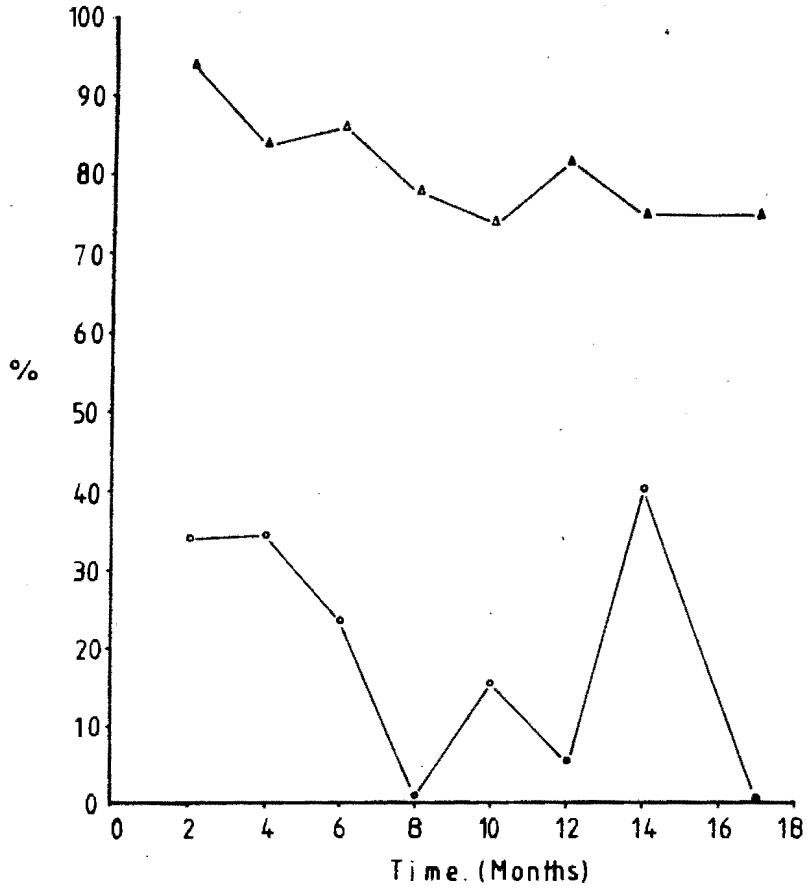


FIGURE 7.36: The germination of fruits while buried at approximately 40 mm on Rhodes Estate. The figure also shows the percentage of apparently viable fruits recovered.

- ∘ % fruits germinated in the field (note: % germination was calculated from the number of fruits recovered).
- ▲ % of fruits recovered (this is also equivalent to the apparent percentage of viable fruits recovered).

TABLE 7.1: The percentage germination of nassella tussock fruits buried at 40 mm on Rhodes Estate. The Table gives the percentage germination for the month of retrieval and the rainfall for that month. The seasons during which retrieval, and therefore monitoring of germination, took place are also shown.

Duration of Burial in Field (Mths)	Month Retrieved	Season Retrieved	Rainfall mm	Percent Germination
2	August 1980	Winter - Spring	20	35
4	October	Spring	30	35
6	December	Summer	85	25
8	February 1981	Summer	-	2
10	April	Autumn	45	15
12	June	Winter	260	5
14	August	Winter - Spring	85	40
17	November	Summer	5	1

The results of the number of fruits germinated while exposed on the soil surface are shown in Figure 7.37. With this group, no germination occurred until the 6th month when 7% was recorded. This then increased in the 8th month, declined in the 10th month and then showed another increase after 12 months exposure. A steady decline was then recorded through 14 months with 4% germination being recorded after 17 months exposure. The results, compared against the season of retrieval (Table 7.2) show a different pattern to that for the buried fruits (Table 7.1). Low to moderately low germination was recorded in summer (December 1980, February 1981 and November 1981). Autumn (April 1981) germination was also low while the spring results were low to moderately low (August 1980, October 1980 and August 1981). The highest germination (32%) also occurred during the month of highest rainfall, 260 mm. There is, however, no correlation between germination and rainfall (Table 7.2).

A further difference between the two treatments, burial and exposure, is the apparent viability of the retrieved fruits. Fruit viability was based on low-power light microscopic examination of the fruits for damage or degradation that would be likely to render the fruits non-viable. The buried fruits (Figure 7.36) maintained their apparent viability for the duration of the experiment. All the buried fruits retrieved appeared to be viable, therefore the percentage retrieval is equivalent to the apparent viability (Figure 7.36).

The situation with the surface exposed fruits is markedly different. These samples showed a decrease in apparent viability from the start and after 10 months only 20% of the retrieved fruits appeared undamaged. After 12 months a figure of 0% viability was obtained. However, this was probably due to fungal attack on the fruits due to delayed counting. A slight increase in apparent viability

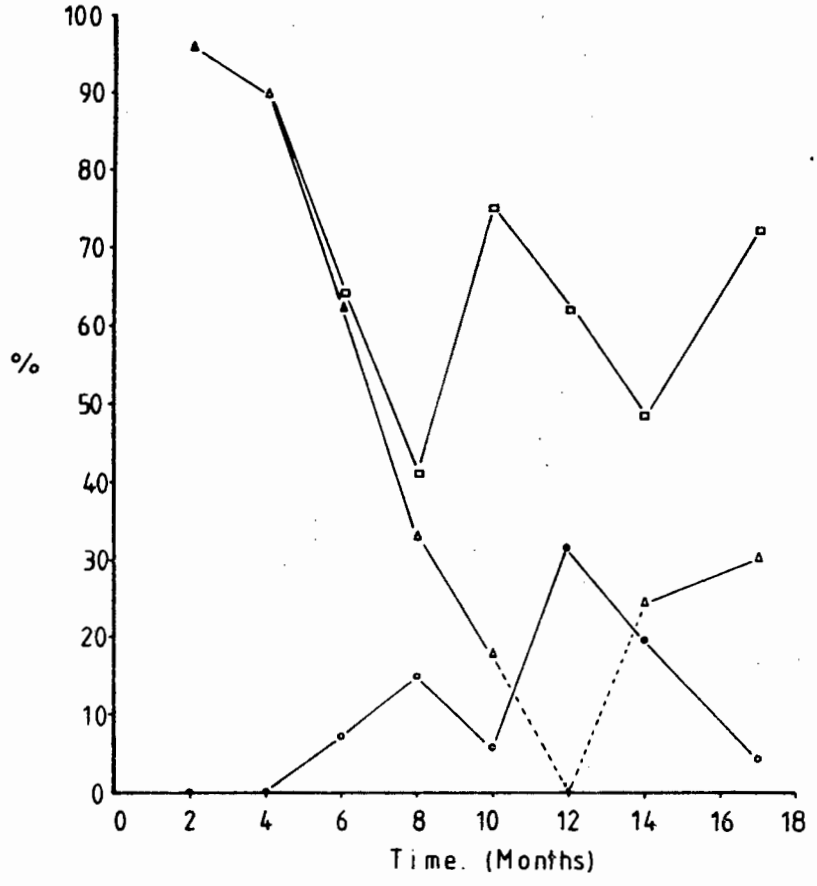


FIGURE 7.37: The germination of fruits while exposed on the soil surface on Rhodes Estate. The graph also shows the percentage fruits recovered and the percentage of apparently viable fruits recovered.

- ∘ % fruits germinated in the field.[1]
- ▫ % of fruits recovered.
- ▵ % of apparently viable fruits.[1] The broken line represents unreliable data.

1. Both these percentages were calculated from the number of fruits recovered.

TABLE 7.2: The percentage germination of nassella tussock fruits while exposed on the soil surface on Rhodes Estate. As in Table 7.1 the percentage germination is shown in relation to the season of retrieval and the rainfall for the month of retrieval.

Duration of Exposure in Field (Mths)	Month Retrieved	Season Retrieved	Rainfall mm	Percent Germination
2	August 1980	Winter - Spring	20	0
4	October	Spring	30	0
6	December	Summer	85	7
8	February 1981	Summer	-	15
10	April	Autumn	45	5
12	June	Winter	260	32
14	August	Winter - Spring	85	20
17	November	Summer	5	4

was recorded in the 14th and 17th months, giving 25% and 30% respectively (Figure 7.37).

This experiment shows that fruits buried at approximately 40 mm on Rhodes Estate do germinate. It also shows that laboratory experiments on the germination of buried fruits (Section 7.7.2) was terminated prematurely. Thirty-five percent germination of buried fruits was recorded in 2 months while laboratory experiments, terminated after one month, had not germinated. Although these field data show that buried fruits do germinate and are therefore available for recruitment, no established seedlings were found in the experimental site, in both the burial and exposure sections. The depth of burial (40 mm) was probably too deep for seedlings to reach the soil surface after germination. The polyester envelope of the surface fruits could have damaged the seedlings and thereby prevented establishment.

The results do show that buried fruits are likely to survive for longer periods than exposed fruits. After 17 months, the buried fruits had 75% apparent viability while the exposed fruits had only 31%. The degradation of the fruit surface, the lemma and palea is shown in Chapter 9. The condition of the fruit surface will be seen to coincide with the above theory, that is, buried fruits showed less damage than the exposed fruits and should, therefore, have a greater chance of survival.

7.13 DISCUSSION

These results have shown that the nassella tussock growing on Rhodes Estate is producing fruits that are difficult to classify into any one pattern of germination. Fruits from tussocks growing in close proximity to each other may produce different patterns of germination. These differences do not appear to be related to morphological

variations in the fruits. The different patterns are seen in response to leaching, temperature and light.

Nassella tussock fruits have been stated to be dormant (Joubert, 1980) or found to be difficult to or slow to germinate, producing about 80% in 800 days (Healy, 1945). The fruits of many other Stipa species appear to be dormant after dispersal from the plant. Ovesnov and Ovesnov (1971) quoted Ponomarev and Zvorygina (1949) as having found that S. joannis and S. rubens, both found on the Russian Steppes, had an 8 month dormant period that could not be broken by stratification. These two species were found to be dormant from July to March, that is, during winter. In America, Dawson and Heinrichs (1952) quoted by Ovesnov and Ovesnov (1971) found S. viridula to be dormant while Ovesnov and Ovesnov (1971) found S. joannis, S. rubens and S. stenophylla to be consistently low germinators. Ovesnov and Ovesnov (1971) found S. capillata to germinate readily. When these species are compared with the results obtained with nassella tussock in this study, it appears that nassella tussock fruits have a very slight dormant period after dispersal. The extent of this dormancy was however found to vary between the different experimental sites on Rhodes Estate.

The dormancy could, in many cases, be reduced by removing the lemma and palea. The effectiveness of this again varied between experimental sites. Removing the lemma and palea in some instances, had a negative effect on the germination as the incidence of fungi on naked caryopses was high. Enhancing the germination of nassella tussock by removing the lemma and palea was used successfully by Joubert (1980). This worker also found that damage to the seed coat increased the germination. This method has been used successfully by other workers on other species as well. Renard and Capella (1976) increased the germination of Brachiaria ruziziensis Germain & Evrard. by removing the lemma, palea and glumes. Hagon (1976) on

S. viridula, Mott (1974) on Aristida contorta and Ovesnov and Ovesnov (1971) on 4 Stipa species all found that either complete or partial removal of the seed coat would enhance the germination. The mechanism whereby the seed coat restricts germination may be either as a mechanical or chemical action. Hagon (1976) suggested that in S. bigeniculata a combination of these mechanisms was operative while in B. ruziziensis, Renard and Capella (1976) felt that the lemma and palea hold chemical inhibitors and have no mechanically restrictive properties. Evidence from the present work suggest that the lemma and palea do not have a mechanically restrictive action as fruits of many samples germinate as readily as the naked caryopses.

Further work carried out to investigate the mode of inhibition and resistance to germinate included the effect of leaching fruits and germination with fruit extracts. The results obtained from leaching experiments suggest that inhibition is probably caused by a water soluble inhibitor or inhibitor complex. Leaching of fruits in running water has been used successfully to enhance the germination of 4 species of Stipa by Ovesnov and Ovesnov (1971). Joubert (1980) germinated naked caryopses on activated charcoal as a means of removing inhibitors. From his results he suggested that an inhibitor was present in the caryopsis and that the lemma and palea restrict either gas or water exchange.

Annual grasses have been forced to germinate by an application of Ethanol (Anon. 1981). Mayer and Poljakoff Mayber (1975) state that alcohol increases germination mainly by influencing water uptake. It could also cause an increase of permeability of gasses, increase light sensitivity or remove an inhibitor. These statements are based on work carried out on Caesalpinia but would probably apply to many other taxa, including grasses. Ethanol, however, appears to have little effect on increasing the germination of nassella tussock from Rhodes Estate.

The bioassay experiments, undertaken to investigate the presence and probable locality of an inhibitor, showed that dormancy is most likely controlled chemically from the lemma and palea. However, the work undertaken is not conclusive because of the variation in germination responses obtained from fruits from Rhodes Estate. More sophisticated separations and assays are required but this experiment has produced results that suggest that a water soluble inhibitor or inhibitor complex is present in the lemma and palea. Landgraff and Juntilla (1979) working on Phalaris arundinaceae Linn. and Mott (1974) on Aristida contorta, using methods comparable to those used in this experiment, found that no inhibitors were present in the seed coats of these two species. Enu-Kwesi and Dumbroff (1980), Goodchild and Walker (1971), Martinez and Santos-Ruiz (1978) and Murphy and Noland (1980) all used similar methods for bioassays of tree seeds and achieved positive results. The results of the nassella tussock bioassay are difficult to compare further because no attempt was made to identify the inhibitor.

The variation in germination found when using the thermogradient bar makes it difficult to classify nassella tussock's temperature requirements. The results from the different sub-sites and the differences found between leached fruits and caryopses produced a wide spectrum of temperatures over which nassella tussock will germinate. Thompson's (1973) description of the character curve of a Mediterranean species are discussed in Section 7.4.2 and shown in Figure 7.17. The experiments using caryopses suggested that nassella tussock is not suited to a Mediterranean type climate and this could be used to explain the limited distribution. However, the leached fruits from sub-site 2.3 produced a wide spectrum of temperatures and showed that nassella tussock is capable of germinating in a Mediterranean type climate. Joubert (1980) found the optimum temperature for the germination

of caryopses to be 28°C after 3 and 5 days on a thermo-gradient bar. This compares favourably with caryopses from Rhodes Estate. Joubert (1980) did not determine the optimum germination temperature for intact fruits.

The light requirements of nassella tussock fruits during germination showed considerable variation. Fruits from sub-sites 1.2 and 1.3 showed marked decreases in percentage germination while sub-sites 1.1, 2.1 and 2.2 showed no light requirement. Two sub-sites, 2.3 and 3.1 were found to be intermediate in their light requirements. Joubert (1980) found that the germination always decreased in the absence of light. Stipa bigeniculata was found to have no light requirement for germination (Hagon, 1976). Ovesnov and Ovesnov (1971) found that S. joannis, S. rubens and S. stenophylla had no light requirements for germination while S. capillata showed an increase in germination in the presence of light. S. nitida, a consistently low germinator was also found to have increased germination in the light (Osborn et al., 1931).

The results obtained when simulating the effect of a fire on the germination of nassella tussock do not coincide with field observations. The results of this experiment suggest that increased germination, in the field, after a fire is as a result of decreased competition. The effect of fire on the germination of other grasses varies. Tothill (in Savage, 1980) found that the germination of buried Heteropogon conturtus P. Beauv. seeds was enhanced by burning. Simtea (in Savage, 1980) found that burning killed all seeds buried at less than 20 mm and decreased the viability of seeds at depths greater than 20 mm. Harper (1977) states that most seeds are buried at depths less than 25 mm. A fire would therefore destroy most of the buried seed store. However, Norton and McGarity (in Savage, 1980) found that temperature changes of more than 10°C were only found in the top 15 mm of the soil and that there was no relationship between the amount of

material burned and the soil temperatures. Ito and Iizumi (in Savage, 1980) found that at 20 mm depth temperatures were not high enough to damage plant material. Further experimentation on the effect of fire on nassella tussock fruits is required before it can be stated definitely that burning itself does not affect the germination directly.

These experiments on the germination of nassella tussock fruits from Rhodes Estate have shown that there is a fairly marked degree of variation in the response of fruits from different experimental sub-sites. This was found even though the sub-sites are in close proximity to each other and presumably all arose from the same source. This suggests that ecotypes may have evolved that are separated by distances as short as 100 metres. These variations make it difficult to categorize the germination requirements of nassella tussock on Rhodes Estate and to compare this to other localities or species. If variation has occurred within the limits of Rhodes Estate then it is probable that this has also occurred in the nassella tussock populations elsewhere in South Africa. Further work would, therefore, be necessary to determine the extent of this variation and to check whether it is controlled genetically or by the microclimate.

The general germination requirements of most of the sites of nassella tussock could be summarized as follows:

1. most fruits are only slightly dormant and possibly have a leachable inhibitor in the lemma and palea. The inhibitor activity appears to vary and thereby cause low or staggered germination.

2. Ageing fruits by one year did not alter the germination significantly.

3. Temperature requirements are broad, from 16°C to 36°C

with germination occurring at 10°C and 40°C.

4. There appears to be no light requirement.

5. Burial in soil decreases the germination, and

6. Fire does not appear to have a direct role in increasing the germination.

CHAPTER 8

TEMPERATURE AND RAINFALL ON RHODES ESTATE

The Geography Department of the University of Cape Town maintains a weather station on the campus. As this is the closest station to the Estate these data were used for the project. Two additional thermohygrographs were stationed on the Estate, one at site 1 and the other at site 3. No equipment was placed at site 2 as it was felt that this site, being in close proximity to site 1, would not have any major temperature variations.

8.1 TEMPERATURE

The temperature for 1979 and the first 7 months of 1980 as recorded at the University of Cape Town are shown in Figure 8.1 and 8.2. No temperature data were available after this period. The curve shows a mild temperature range with a summer mean maximum of 25°C in February 1979. In 1980 the highest mean maximum recorded was 24°C in March. The corresponding mean minimum temperatures were 18°C and 17°C respectively. The mean minimum temperatures in winter were 10°C in July and September 1979. The maximum summer temperature was 34°C recorded in February 1979 while the lowest recorded temperature was 7°C in June 1980 (Figures 8.1 and 8.2).

The temperatures recorded on Rhodes Estate at the two experimental sites were very different to those on the Campus. A direct comparison is not possible as the field recordings were carried out during 1981. Figure 8.3 shows the temperatures as recorded at site 1. The

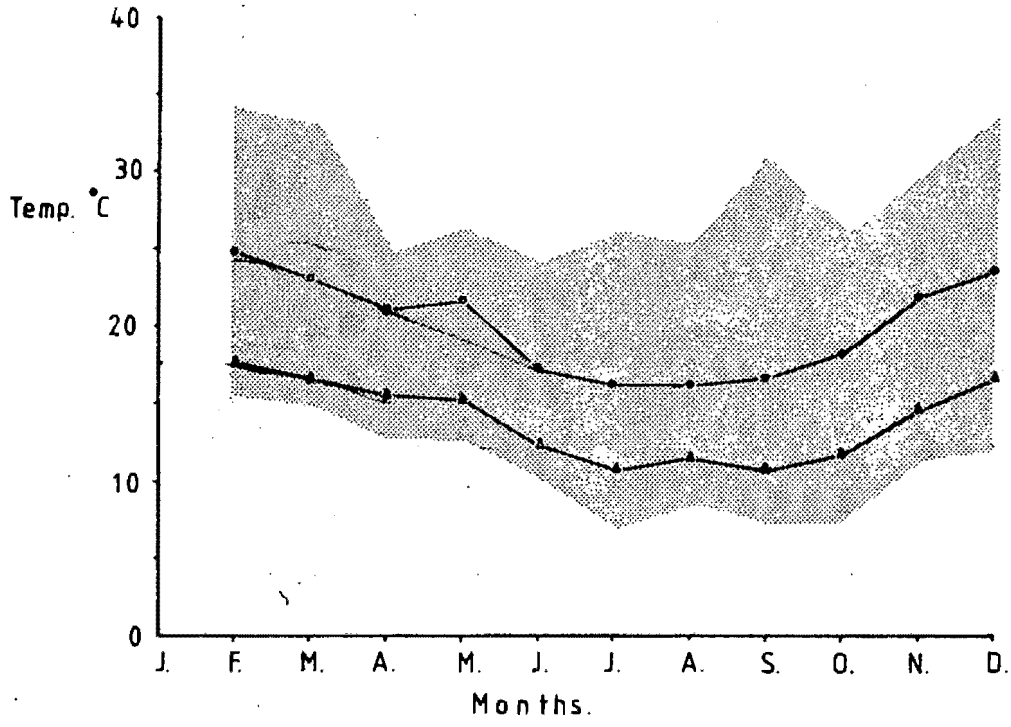


FIGURE 8.1: The monthly mean maximum (◦) and minimum (▵) temperatures as recorded for 1979 by the Geography Department, University of Cape Town. The shaded area represents the fluctuation about the means and shows the highest and lowest recorded monthly temperatures.

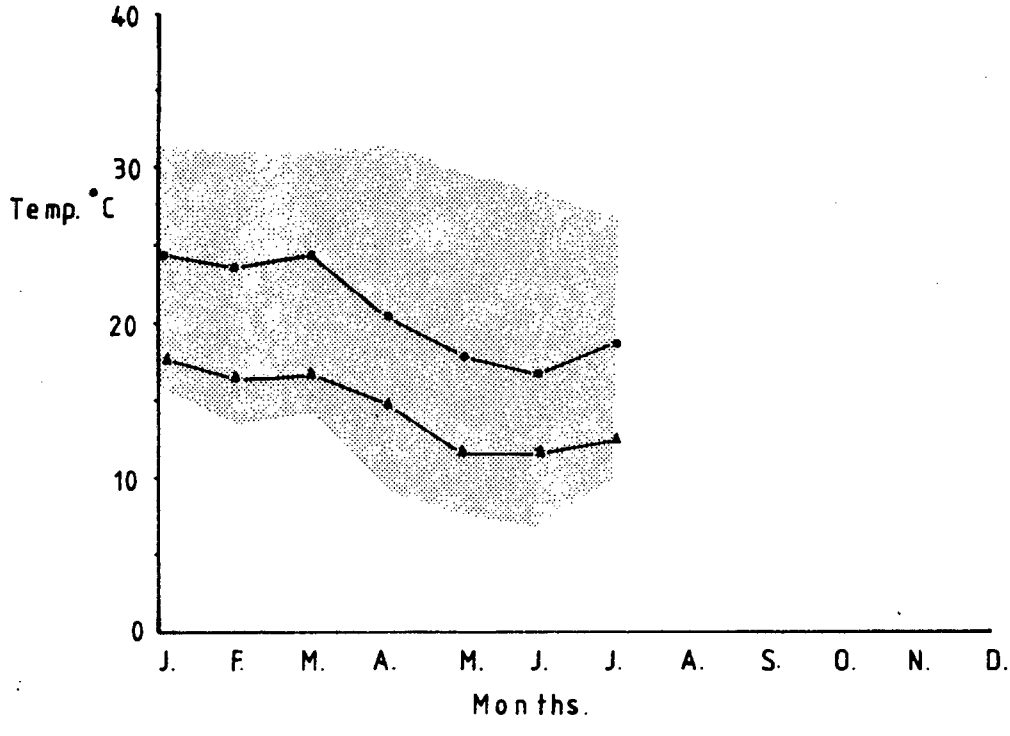


FIGURE 8.2: The monthly mean maximum (◦) and minimum (▵) temperatures as recorded for January to July 1980 by the Geography Department, University of Cape Town.
The shaded area represents the fluctuation about the means and shows the highest and lowest monthly temperatures.

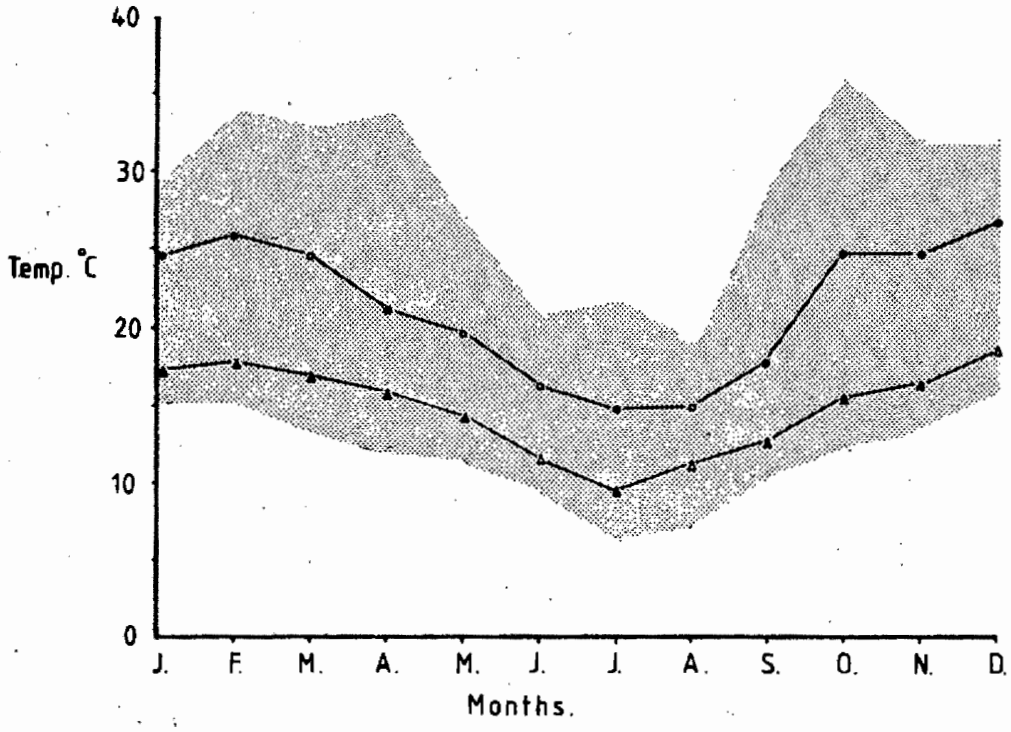


FIGURE 8.3: The monthly mean maximum (◦) and minimum (▵) temperatures as recorded for 1981 at site 1. The shaded area represents the fluctuation about the means and shows the highest and lowest monthly temperatures.

highest summer mean maximum was 26°C in December 1981 while the highest daily temperature recorded was 36°C in October 1981. The lowest mean minimum temperature at 9°C was recorded in July 1981. The lowest daily temperature was 6°C, recorded in July 1981.

The temperatures at site 3 (Figure 8.4) were recorded from November 1980 to August 1981. These results show only slight differences from those of site 1 (cf. Figure 8.3 and 8.4).

8.2 RAINFALL

Rainfall data were not collected on the Estate because the differences that were likely to be found between the Estate and the University did not warrant the security procedures for rain gauges in the field. The rainfall as recorded at the University is expressed in millilitres per month in Figure 8.5. Rainfall figures for both 1980 and 1981 are shown. The fainfall pattern in 1980 was unusual in that the summer rainfall was relatively high while little rain fell during the normally wet winter months. In July 1980 only 15 mm fell while in April and December of the same year 118 and 80 mm respectively were recorded. The rainfall figures for January, February and March 1981 were not available. In June 1981, 262 mm and in July 194 mm were recorded. The summer rainfall for 1981 was low, with only 8 mm being recorded in both October and November.

The rainfall pattern of the 1981 season was more typical of the Cape Peninsula, being a summer drought-winter rain region. However, most of its field growth rate data were collected in 1980 and could therefore be different from other years with a normal rainfall pattern. Nassella is, however, reported to be adapted to dry climates (Healy

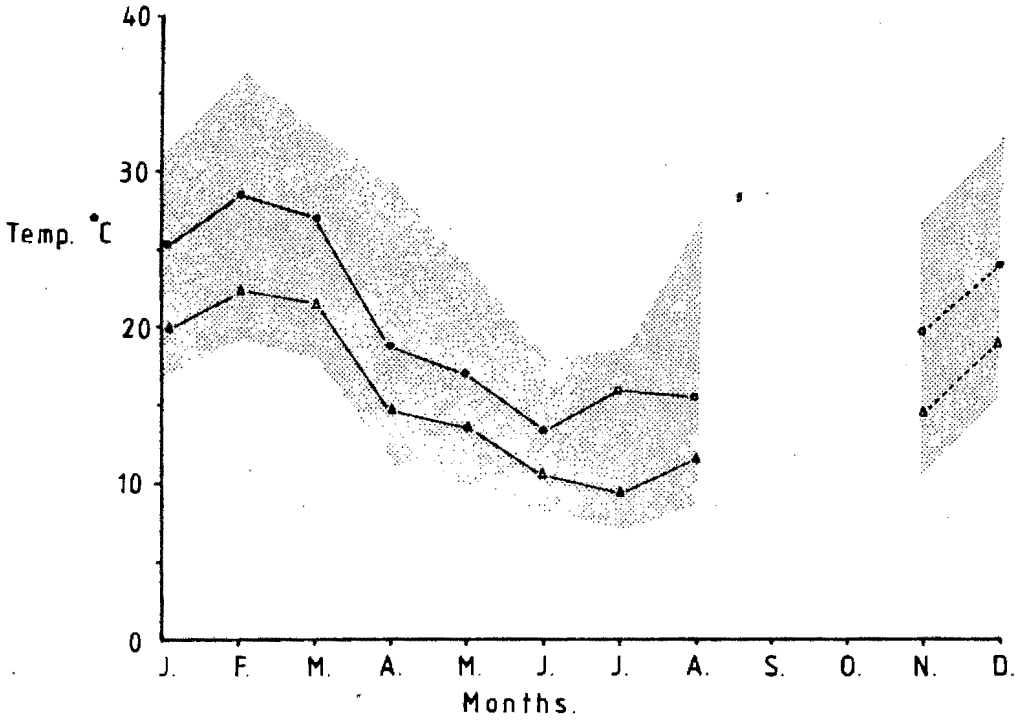


FIGURE 8.4: The monthly mean maximum (∘) and minimum (▵) temperatures as recorded from November 1980 to August 1981 at site 3.
The broken line shows the 1980 temperatures.
The shaded area represents the fluctuation about the means and shows the highest and lowest monthly temperatures.

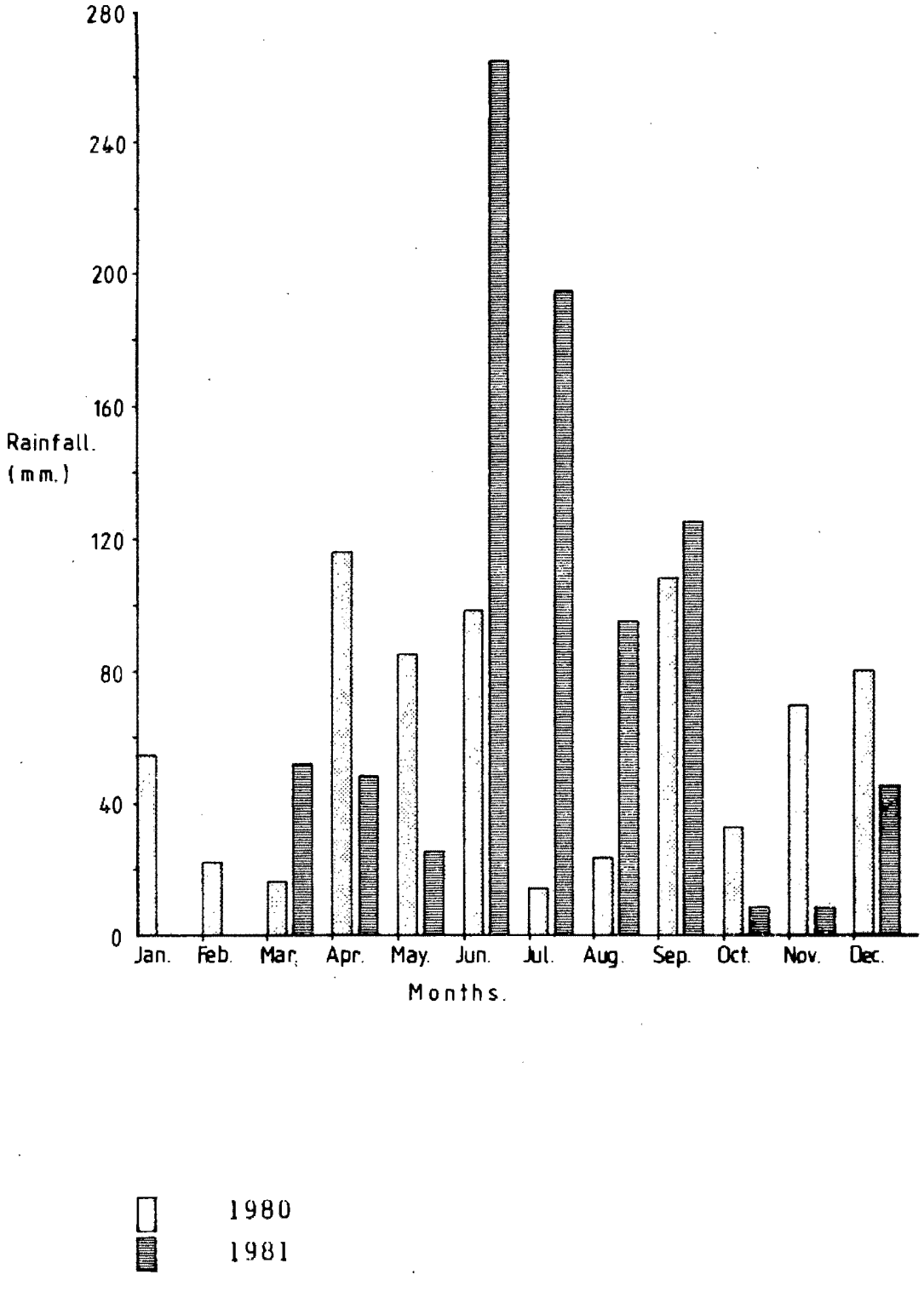


FIGURE 8.5: The monthly rainfall (in mm) as recorded by the Geography Department, University of Cape Town.

1945) and should, therefore, not be adversely affected by a dry winter.

CHAPTER 9

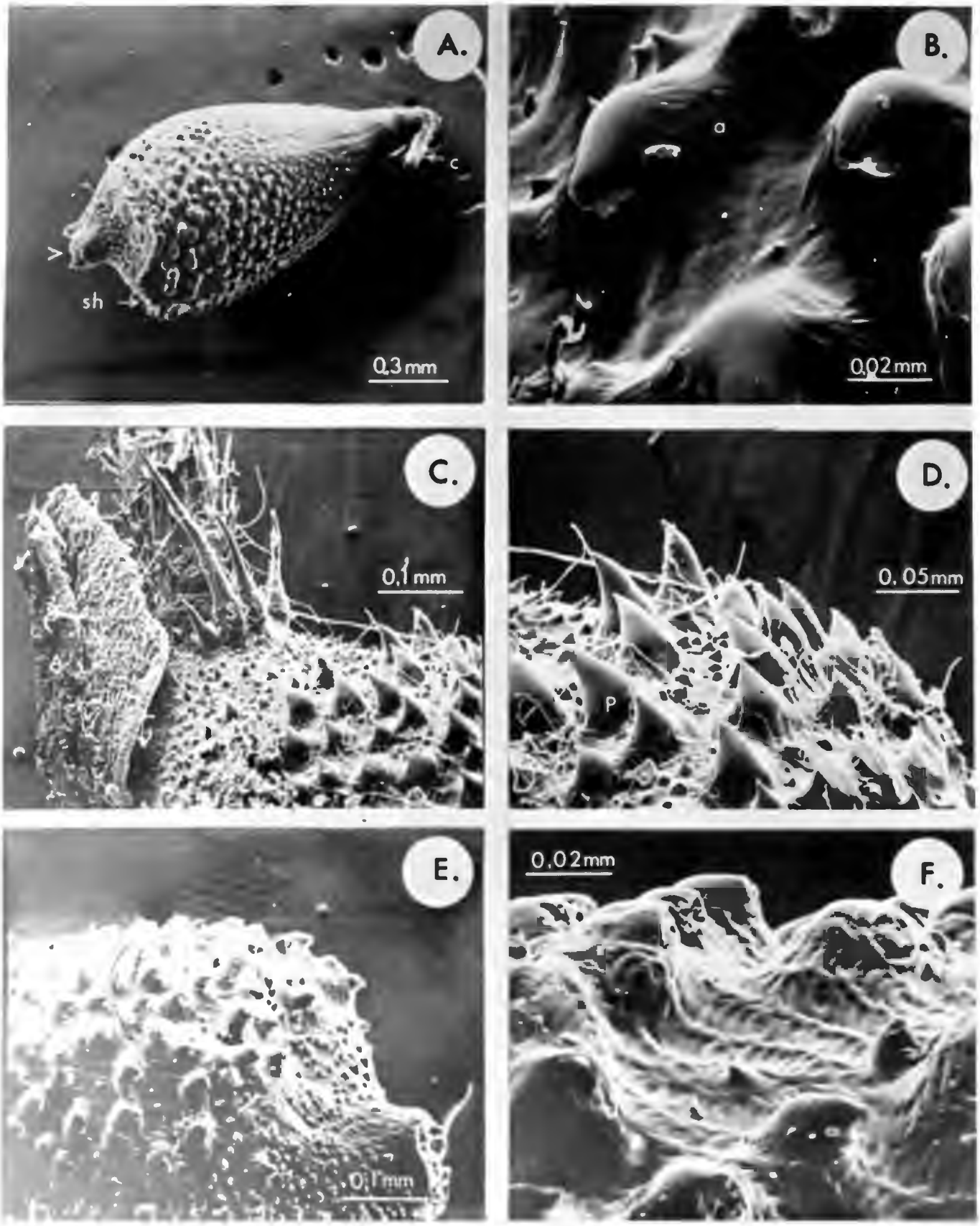
FRUIT STRUCTURE

A limited study of the external fruit structure was undertaken, using a Scanning Electron Microscope. The main aim of this study was to determine whether there were any additional differences between fruits with different shapes, those with different colours and between Eastern and Western Cape fruits.

9.1 GENERAL FRUIT STRUCTURE

In Plate 9.1 fruits from both Rhodes Estate and Thomas River are shown. No major differences between overall shape-variants or colour variants were found while only a slight differerecebetween Rhodes Estate and Thomas River fruits was found. Plate 9.1 A shows a fruit from Thomas River. The awn has been removed and only part of the callus (C) remains. This fruit shows the general oblong shape with a fairly prominant shoulder (sh) just below the awn (>). The fruit is covered by small protrusions or papillae. In part C of Plate 9.1 a fruit from sub-site 1.3 is shown. This is a fruit that was presumed to have opened for fertilization, that is, the anthers and stigmas were exposed. On the left of the plate, just below and against the awn is the remains of the anthers (A). Another feature, not found in all fruits, is the presence of long spines (S) at the base of the awn (cf. Plate 9.1 A, C and E). Part D of Plate 9.1 shows the shoulder of the fruit shown in Part C. Long curved papillae (P) are shown. The papillae are not always seen to be this long or sharp and are often blunt protrusions from the surface. A fruit from Thomas River (Plate 9.1 E)

PLATE 9.1 The surface structure of nassella tussock fruits. (A.) The general shape of a fruit from Thomas River, showing the base of the awn (>), the shoulder (sh) and the remains of the callus (c). (B.) The structure of the coat between the papillae on a fruit from Rhodes Estate. (C.) The area at the base of the awn showing elongated spines (S) and the remains of the anther (A) (Rhodes Estate). (D.) The large papillae (P) on the shoulder with smaller recurved ones between these (Rhodes Estate). (E.) The more rounded papillae on a fruit from Thomas River. (F.) The reticulated pattern between the papillae of a fruit from Thomas River.


A.
c
v
sh
0,3 mm
B.
a
0,02 mm
C.
0,1 mm
D.
0,05 mm
P
E.
0,1 mm
0,02 mm
F.

is seen to have rounded papillae without the spines at the base of the awn. The area between these papillae is usually covered with smaller papillae, curved in the opposite direction (Plate 9.1 C, D and E). These smaller papillae are most common on the shoulder and the neck, the area just below the awn.

The fine structure of the area between the papillae differs between the Rhodes Estate and Thomas River fruits. In the Rhodes Estate fruits this area is seen to be smooth (Plate 9.1 B) while in the Thomas River fruits this can be seen to be reticulated (Plate 9.1 F). It is possible that this is caused by one sample being more desiccated than the other. It is felt, however, that this is not the case as both samples received identical treatment.

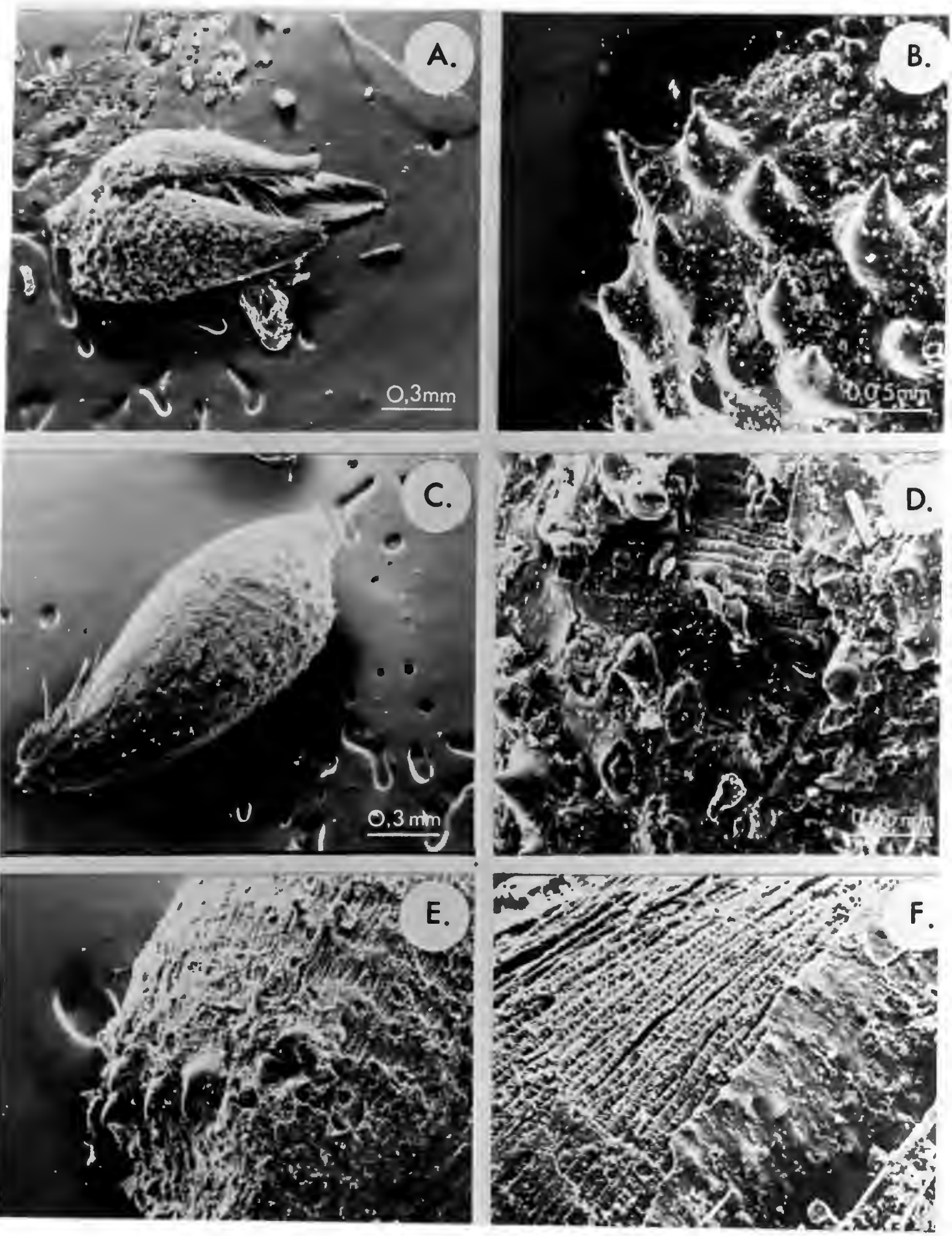
9.2 SURFACE STRUCTURE OF FRUITS EXPOSED IN THE FIELD

Plate 9.2 A shows the remains of a partially germinated fruit that was retrieved after 2 months burial in the field. The feature of importance here is that the lemma surface is intact although it has been split by the emerging seedling. After 6 months burial there is little change in the appearance of the lemma (Plate 9.2 B). The surface structure of this fruit, except for particles of dirt, is no different to that shown in Plate 9.1 E. There was no change in the structure of the lemma after 8 months burial.

The fruits examined on the soil surface show a greater degree of surface damage. In plate 9.2 C and D a fruit exposed for 4 months is shown. Plate 9.2 C shows the whole fruit, with marked decay of the surface. The surface appears to be cracking and peeling away to reveal a fibrous layer (Plate 9.2 D). After 8 months exposure

PLATE 9.2: The effect of exposure in the field on the surface structure of nassella tussock fruits. (A.) A fruit buried for 2 months. (B.) The condition of a fruit after 6 months burial. (C.) and (D.) The condition of the fruit surface after 4 months exposure on the soil surface. (E.) and (F.) The condition of the fruit surface after 8 months exposure on the soil surface.

Note the lemma suture in F and the longitudinal fibres exposed in D and F.


A.
0,3mm
B.
0,05mm
C.
0,3 mm
D.
E.
F.

this process has extended to the extent that large areas of the fruit surface have been degraded to expose the fibrous layer (Plate 9.2 E and F). Plate 9.2 F shows the extent of degradation after 8 months with a large area of fibres exposed near the lemma suture. The fibres can be seen to run longitudinally down the length of the fruit.

No analyses were undertaken to identify the nature of the surface layer that is being removed. However, when compared to seed surface structures in Kaufman et al. (1972), it appears that it could be a silicon based compound. The papillae appear to be constructed of the same material (Plate 9.2 D and E).

GENERAL DISCUSSION

One of the main objectives of this work was to study nassella tussock with a view to identifying possible avenues for control. The experiments revealed variation in behaviour of the plants found on Rhodes Estate. Some of these variations, such as growth rates and flowering times can be attributed to micro-habitat differences. Other variations, such as those found in germination, are not as easily explained in this way. These variations make general predictions difficult. This in turn causes difficulties in recommending control measures.

Variations that can be attributed to micro-habitat differences in the Estate are growth rates and phenology. These two criteria appear to be closely linked. The largest portion of Rhodes Estate is hot and dry and is comparable to experimental sites 1 and 2. From these sites, the period of maximum growth was seen to be in spring and early summer (see Section 4). This was followed closely in mid-summer by the onset of flowering (see Section 6). It was also seen that the relative growth rate declined while the floral cycle advanced. In the moist areas, as at site 3, the whole cycle was retarded, with the period of maximum growth occurring in mid-summer and flowers being produced in late summer. Therefore, if a control programme is aimed at preventing seed set it would have to be initiated in October in the hottest, driest areas, later in moister sites. This time would also vary from year to year as annual climatic variations cause shifts in the onset of flowering (Healy, 1945).

As discussed in Section 5, variations also occurred in tussock colour and shape. This also appeared to be closely

related to micro-habitat differences. Variations in fruit production followed very similar patterns. Tussocks growing in exposed dry areas were seen to be short, brown leaved and to have large basal circumferences. These tussocks had the highest fruit production. In moist, sheltered areas, the tussocks were a deep green with long leaves and small basal circumferences. These tussocks produced few fruits.

A further variation in fruit production was the appearance of cleistogamy (see Section 6.4). This appeared to be directly related to the degree of exposure to the sun or the degree of shading. This appeared to be effective at the level of inflorescences and not necessarily whole tussocks. Tussocks found in open areas were seen to have fewer cleistogamous flowers than shaded ones. Evans (1964) stated that cleistogamy is often facultative and that it occurs under adverse conditions in the late stages of floral development. Stipa leucotricha Trin. + Rupr. could produce both cleistogamous and chasmogamous florets on the same inflorescence (Evans, 1964). This was also seen to occur in nassella tussock on Rhodes Estate. Evans (1964) stated that cleistogamy is caused in some Stipa species by drought or low temperature and by low light intensity in Bromus carinatus Hook. + Arn. Other factors that have caused cleistogamy are short day length, low nutrition and short days while plants are still young (Evans, 1964). Observations showed that cleistogamy in nassella tussock resulted in a variation in the shape of the fruit. Cleistogamous fruits were seen to be short and fat while cross pollinated fruits were long and thin. No mention of fruit shape variations resulting from cleistogamy was found in the literature. Wells (1975) found that fruit shape varied along a north-south transect in South America. To the north the fruits were found to be short and fat while in the south the form became more variable with long thin fruits being common. Fewer inflorescences were produced per tussock in the south (Wells, 1975). Wells

(1975) stated that in his opinion the short fat fruit was the invasive form and that it was this form that was present in South Africa. In New Zealand and Australia the short fat form is also found. However, there is some variation of fruit shape in these two countries (Wells, 1975).

If the observed pattern on Rhodes Estate (that is, short fat fruits have been produced cleistogamously) is extrapolated, then in the more northern areas of South America nassella tussock reproduces cleistogamously. However, no habitat data are available so it is not possible to relate this to the degree of shading. This, however, suggests that cleistogamy is very common in nassella tussock and is unlikely to be as a result of adverse conditions. Further observations on habitat and cleistogamy as well as experiments are required to investigate its occurrence and effect on the reproductive ability of nassella tussock.

The comon occurrence of cleistogamy in nassella tussock on Rhodes Estate would have resulted in extensive inbreeding. A limited gene-pool is therefore available for adaptive changes and variation. This could result in a decreased reproductive fitness which would make nassella tussock less competitive. Decreased reproductive fitness would explain the limited spread of nassella tussock from Rhodes Estate. However, as discussed earlier, Wells (1975) found short round fruits to be common in other locations. This would mean that those areas also have a less aggressive form. This contradicts the findings of Wells (1975) that these fruits are the aggressive form. It would, therefore, appear that inbreeding through cleistogamy has not decreased the reproductive fitness of nassella tussock.

The variation most difficult to explain is that found in the germination response of fruits. The percentage and

rate of germination, the effect of leaching and the removal of the lemma and palea was seen to differ between sites. These differences were not always constant. The major difference was the apparent dormancy of fruits. Fruits from site 2 were seen to germinate readily. Sub-site 1.3 and 3.1 had slightly dormant fruits. The fruits from the tussocks approximately 100 metres south east of sub-site 1.1 were found to be very slow germinators (see Section 7). These differences manifested themselves in an area of 450 ha and from tussocks as close as 100 metres apart. These differences could not be attributed to any major physical differences between the localities. They could, however, be caused by local soil differences although this seems unlikely as the soils of the Estate are fairly uniform (see Figure 2.1). However, the evolution of ecotypes over very restricted distances is not uncommon. Antonovics et al. (1971) reviewed the development of ecotypes in plants in response to heavy metal toxicity in soils. Gregory and Bradshaw (1965) discussed the development of resistance of Agrostis tenuis Sibth. to heavy metals.

Bradshaw (1959) found that variation was controlled by the environment but that distances of less than 50 m were sufficient to isolate populations from one another. The variations found in A. tenuis by Bradshaw (1959) include differences in vegetative structures, seed emergence and maturation, yield (productivity) and mode of growth and spread. Plants can, therefore, adapt to micro-habitat differences over very small distances. The presence of cleistogamy and therefore inbreeding assist this process of evolution over limited distances. Cleistogamy effectively isolates the populations irrespective of distances.

From this discussion it can be seen that it is quite possible that nassella tussock has evolved differences within the Rhodes Estate population. Differences that have been found are variations in germination patterns and

different growth rates between sites 1 and 2 and site 3. The difference in growth rates was not investigated further so there are insufficient data to decide whether this is an evolved response or not. This would require experiments with transplanted tussocks and seedlings similar to those carried out by Bradshaw (1959) and Horsman et al. (1979). It seems probable that the germination response is a genetically fixed trait as this was consistent throughout the experiments.

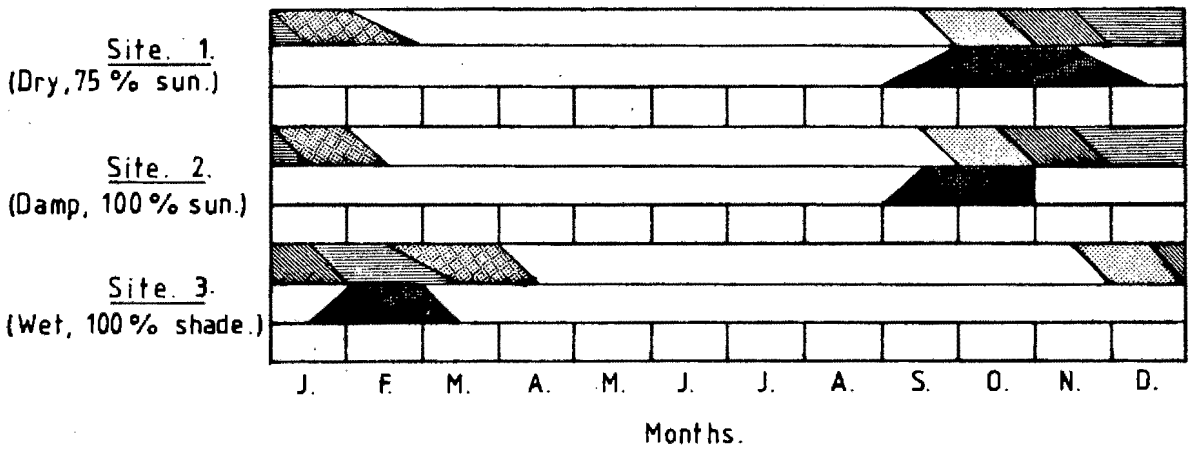
The only morphological character that was investigated was the fruit shape. It has been stated earlier in this discussion that this phenomenon is as a result of cleistogamy. This character does not appear to be a micro-habitat variation but rather a response to the prevailing light intensity. The condition of the tussocks grown under semi-controlled conditions (see Section 5) suggest that other morphological variations are unlikely to be genetically fixed. These tussocks were grown from fruits from different experimental sites (that is, different micro-habitat conditions) but all the tussocks produced under the same set of experimental conditions were similar in appearance. It was not possible to trace a tussocks origin by its phyiscal appearance.

The life cycle of nassella tussock to be given here is a generalization for the reasons discussed above. The variations just discussed make it impossible to give a pattern that will hold true for all sites and all climatic variations. This cycle was based on the results obtained from sites 1 and 2 as it was felt that these were most representative of the whole Estate.

Nassella tussock will germinate under a wide range of temperatures (from 10°C to 46°C) but has an optimum germination temperature in the range 24-32°C with an average of 28°C. Nassella tussock is therefore not adapted to a

Mediterranean type climate temperature range of 10-22°C (Kendrew, 1937) but is adapted to Rhodes Estate as this site has higher temperatures (see Section 7.4). Germination in the field occurs mainly in spring but does continue throughout the year. The tussocks appear to be slow growing and do not reach reproductive maturity in one year. The peak growth season is in spring and early summer with floral production occurring from October through to December. Fruit dispersal occurs in January and February (Figure 10.1). The fruits produced are variable in size, shape, colour and in their degree of dormancy.

The control of nassella tussock or methods to control it were not studied. However, field experiments and observations highlighted some factors for control. Fencing of the experimental sub-sites restricted grazing in these areas for 2,5 years. In site 2 the growth of the other tussock grasses was so great in 1,5 years that it prohibited the monitoring of the 1981 flowering season (see Section 6.2). One plot 4 x 4 metres was fenced in a sparsely infested area of mixed herbaceous vegetation but was not used for experimental purposes. Although no data were collected on individual species, it is interesting to note that the vegetation within this plot was approximately 100 mm taller than that in the surrounding area after 2,5 years. This is significant when the vegetation consists of prostrate herbs, grasses and small shrubs. No nassella tussock seedlings were found in this plot and most of the existing tussocks were being smothered. This shows the importance of the maintenance of a good ground cover in restricting the growth and spread of nassella tussock. This is exemplified further by comparisons of the ground cover of Rhodes Estate and the surrounding lands. The surrounding properties have a better ground cover and a lot less nassella tussock than Rhodes Estate. In Section 3.1.1 the regrowth of nassella tussock from seed after clearing was discussed. In that section it was stated that in many cases nassella tussock was the only



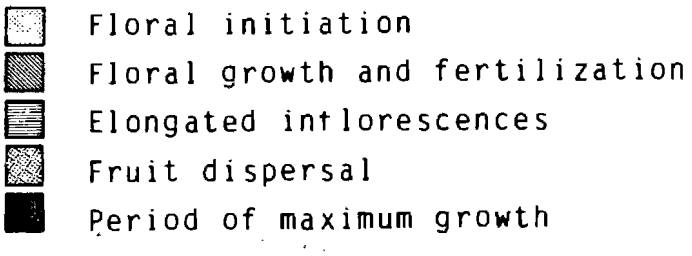


FIGURE 10.1: A diagramatic representation of the flowering cycle of the tussocks in the experimental sites. The period of maximum tussock growth is also shown. Unshaded areas represent periods of no productive activity and limited growth.

plant to appear after the clearing operation. All these points indicate the necessity of a revegetation programme to be part of a control operation and for improved management of the established vegetation.

To accomplish this it could be necessary to divide the Estate into camps (as has been done in the north-east corner bordering De Waal Drive) and to restrict the movement of the fallow deer. The range of the herd of donkeys and horses should also be restricted. Human access cannot be stopped due to the open nature of the area. It would, however, be preferable if human movement could be restricted to certain areas or to selected walking trails on the Estate. The control programme, to date, has been one of hand grubbing tussocks with limited use of chemical sprays. The nature of the Estate and infestation do now allow for an overall chemical spray. However, in many areas, backpack prays would be ideal to combat the dense stands of young seedlings. In many of the inaccessible areas, however, grubbing remains the only means of control. Whether the control programme uses grubbing or chemical sprays it is essential that it is followed up correctly with all areas being revisited annually. At present many areas are cleared every second or third year. This results in the seedlings maturing and producing fruit and thereby lengthening the duration of the programme. A further problem is that control is often seen as preventing nassella tussock from setting seed and not the removal of all the tussocks. This results in a control programme that starts in September, just before floral initiation and stops in February after seed dispersal. This means that actual control is only being carried out during six months of the year. To control nassella tussock it is necessary to remove all the tussocks and then to maintain the progamme so that all new occurrences are removed before they set seed.

Healy (1978) reviewed the situation of nassella tussock

in South Africa. He discussed control measures that are applicable to nassella tussock in general. However, some of these, such as heavy tree planting and bull-dozing, are not suitable to Rhodes Estate. Healy (1978) stated the importance of veld management in controlling nassella tussock. Other methods of control that appear to have limited value in some situations include the use of grazers to prevent nassella tussock from flowering (Campbell et al., 1979; Campbell and Holst, 1978). This method is suited to a very dense infestation in agricultural situations. It is not applicable to Rhodes Estate due to the scattered nature of the infestation. The fallow deer have been seen to graze nassella tussock. This was seen in the moist valleys where the tussocks appeared more succulent than in the open areas. This was, however, an occasional occurrence and could not be regarded as a possible means of control.

By comparison to infestations in the rest of South Africa (Wells, 1974), in New Zealand (Dingwall, 1969 and Healy 1945) and in Australia (Campbell, 1965) the problem on Rhodes Estate is small. It appears that there has been little spread since the plant was first recorded on Rhodes Estate in the mid 1930s. This suggests that the nassella tussock on Rhodes Estate is either less aggressive or is not ideally adapted to the area. Control is, therefore, simplified in that the size of the infestation does not appear to be increasing. Therefore, with a concerted effort it would be possible to control the nassella tussock on Rhodes Estate.

Except for the variation found in nassella tussock on Rhodes Estate, there do not appear to be any major differences between this site and others that have been studied. The growth rates, habitat and floral cycle are similar to that discussed by Campbell (1965) and Healy (1945). The germination, where comparisons are possible, compares favourably with that discussed by

Joubert (1980) but is more rapid than that found by Healy (1945). The data available on the control of nassella tussock at other localities are, therefore, probably adaptable for use on Rhodes Estate. The adaptations required would be based on land use differences because most control procedures have been designed for agricultural situations. Most of the ecological data (Healy, 1945, Campbell, 1965; Dingwall, 1969) and germination data (Healy, 1945 and Joubert, 1980) are significant for use on Rhodes Estate.

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