ECOLOGY PROJECT

A PRELIMINARY INVESTIGATION OF THE PROPOSED SURVIVAL MECHANISM OF *THAMNOCHORTUS* SPP. IN RESPONSE TO FIRE.

AMANDA GEEL
BOTANY HONOURS
1979.

CONTENTS

ABSTRACT

Post-fire sprouting as a proposed survival mechanism was investigated in two *Thamnochortus* spp. (Restionaceae). Increased nutrient availability and phytomass removal damage were simulated as important post-burn effects.

Though the preliminary results obtained did not appear to substantiate the sequence of re-growth observed in the field, this was felt to be due to the omission of heat stress injuries being simulated. In addition the study revealed that a number of factors could influence the results, and suggestions for further work are presented.

1. INTRODUCTION

The long warm and dry summers of mediterranean climate zones provide ideal conditions for the development and spread of fires across the landscape. The response of the vegetation in these areas to fire is probably one of the major features common to these ecosystems (Gill and Groves, 1979). Gill (1975, 1977) considers there to be four major categories of fire adaptation: bud protection and sprouting; fire-induced flowering; on-plant seed-storage and fire-stimulated dispersal; and in-soil seed storage and fire-stimulated germination (see also Hanes, 1977). These traits are adaptive to fires in that they enhance survival and/or reproduction (after Dobzhansky, 1956).

All these fire-adaptive traits have been recognized in fynbos (see Kruger, 1977). However, in this report I am concerned solely with the first trait - particularly resprouting from rhizomes at or near the soil surface. This feature predominates in the perennial graminoid herbs - the Restionaceae. The family Restionaceae is comprised of wiry aphyllous hemicryptophytes which are invariably present in the fynbos and are the dominant or co-dominant physiognomic element (Taylor, 1977; 1978).

In the field, it had been noted that some Restionaceous species which produce shoot growth off culms (Figure 1a), were present only as bushy shoot growths in the immediate post-fire phase of succession (Figure 1b), and only later did culm growth occur (Moll, pers. comm.). The possible ecological significance of this phenomenon as a survival mechanism was investigated in the genus Thamnochortus, Berg. in a selected Mountain Fynbos Community (Veld Type 70; Acocks, 1953).

The effects of phytomass removal and soil nutrient status were the factors simulated, as fire affects the vegetation, litter and soil (De Bano

and / -

Figure 1a: Thamnochortus dichotomus plant exhibiting shoot growth off culms, and died back bushy clump growth.

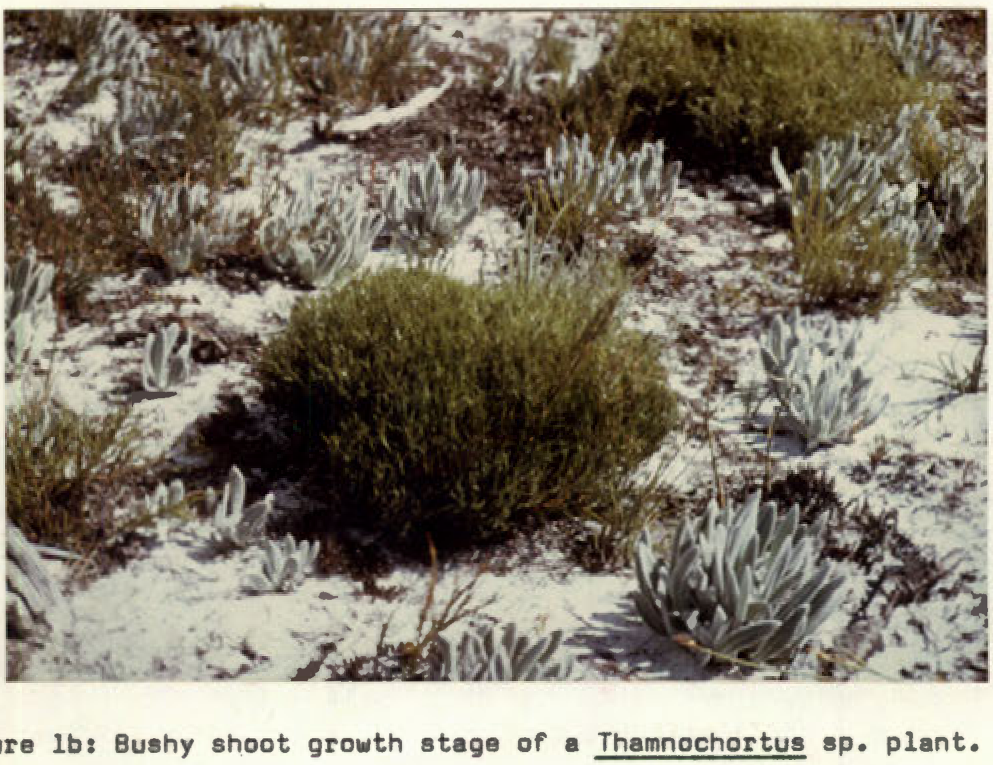

Figure 1b: Bushy shoot growth stage of a Thamnochortus sp. plant.

and Conrad, 1978). There may be direct consumation of all or part of the standing plant material and litter, as well as organic matter in the upper layers of the soil, and nutrients in the organic matter are either made more available or lost from the site (e.g. gaseous loss of nitrogen; Christensen, 1973; Grier, 1975). Generally, however there is greater nutrient availability (De Bano and Conrad, 1974).

1.1. Description of study sites

Individual plants were marked at sites in immature and mature stands of mountain fynbos communities at Silvermine Nature Reserve, Cape Town, South Africa. Both stands occurred on Table Mountain Sandstone-(TMS) derived soils, and the immature stand was situated on a level site, while the mature stand was situated on a gentle south-west facing slope. The mature stand had last been burnt approximately four years ago, while the immature stand was burnt on the 8th June, 1978, six weeks after being bush cut, by the staff of the (City Council controlled) Nature Reserve.

Predominant species in the immature stand are Aspalathus sp., Struthiola sp., Helichrysum sp., Hypodiscus aristatus, Staberhoa curnua, Thamnochortus punctatus and T. dichotomus (Figure 2a).

In the mature stand common species recorded were Struthiola sp., Stoebe sp., Lobelia sp., Phylica sp., Euryops sp., Rhus lucida, Metalasia muricata, Helichrysum zeyheri, Crassula sp., Leucondendron laurifolia, Leucospermum conocarpodendron and various Restio, Elegia and Thamnocortus spp. (See Figure 2b).

Figure 2a: Immature stand - burnt June 1978.

Figure 2b: Mature stand - burnt approximately four years ago.

2. METHODS

2.1. Immature Stand

The following treatments were performed on individual *Thamnochortus punctatus* or *T. dichotomus* plants on the 5/4/79, and on plants in a replicate site adjacent to the original on the 5/5/79:

Table 1: Treatments employed on individual *Thamnochortus* sp. plants in sites in an immature mountain fynbos community.

TREATMENTS	ORIGINAL SITE	REPLICATE SITE
1. Culm growth removed to ground level - no fertilizer	3 plants	3 plants
2. Culm growth removed to ground level - fertilized	3 plants	1 plant
3. Entire plant clipped to ground level - no fertilizer	1 plant	2 plants
4. Entire plant clipped to ground level - fertilized	2 plants	1 plant

2.2. Mature Stand

Again, two sites were selected, situated on either side of gulley. Treatments were performed on the 5/4/79 at the original site and on the 5/5/79 at the replicate.

Table 2: Treatments employed on individual *Thamnochortus* sp. plants in sites in a mature mountain fynbos community.

TREATMENTS	ORIGINAL SITE	REPLICATE SITE
1. Culms cut to height of 10 cm - no fertilizer	2 plants	2 plants
2. Culms cut to height of 10 cm - fertilized	2 plants	2 plants
3. Entire plant clipped to ground level - no fertilizer	2 plants	2 plants
4. Entire plant clipped to ground level - fertilized	1 plant	2 plants
5. Entire plant clipped to 1 cm below ground level - no fertilizer	1 plant	2 plants
6. Entire plant clipped to 1 cm below ground level - fertilized	2 plants	2 plants

At both stands plants were marked by an adjacent stake and tag of coloured wool. Fertilized plants were denoted by two wool tags.

Fedmis Group I 3 - 2 - 1 fertilizer (i.e. 12,5% N; 10,3% P; 4,0% K) was applied every month during the study period April - August, at a rate of 0,3g per plant (c.345 kg ha^{-1}).

2.3. pH

A standard method of pH determination was employed (from Parsons, 1978 unpub.) outlined as follows. To 25g of soil, 50 ml of 0,01M $Ca\ Cl_2$ was added and the mixture stirred for an hour until thoroughly mixed. The pH was then read from a pH meter, standardized against pH4 and pH7 buffer solutions.

2.4 Determination of organic matter

The method employed for determination of organic matter was a modification of that explained by Hess (1971). A 20g soil sample was weighed into a crucible and then placed in an oven at 80°C for approximately 5 hours to obtain soil dry weight. The samples were then placed in a muffle furnace for 8 hours at 450°C. The weight loss was expressed as percentage organic matter.

2.5 Phosphorus determination

'Plant available' phosphorus was determined by means of the Murphy and Riley (1962) adaptation of the molybdate blue method. Soil samples of approximately 8g were shaken for 1 minute with Bray 2 extracting solution consisting of 0,03N ammonium fluoride in 0,1N Hcl at a soil / extractant ratio of 1: 7,5.

Total / -

Total phosphorus determination was based on Hess's (1971) method. Approximately 2g of soil (2mm sieved) were heated in a muffle furnace at 240°C for 1½ hours. Samples were then digested in concentrated HCl for 30 mins, and diluted aliquots were measured for total phosphorus by the Murphy and Riley method described above.

Only immature stand soil samples were analysed.

2.6 Relative photosynthetic rate

The method used was a modification of that employed by Voznesenskii, Zalenskii and Austin (1971). Shoot or culm growth were enclosed in a 10 x 15 cm plastic bag with an open glass container holding 1 ml of 50 µCi $Na^{14}CO_3$. The apparatus was then made air tight, and 1 ml 10% lactic acid was injected into the container to generate $^{14}CO_2$ and the hole sealed. The plants were left to assimilate the $^{14}CO_2$ for varying periods of time i.e. 10 minutes, 25 minutes and 45 minutes. The reaction was stopped with excess (~2mls) 4NKOH. The radioactive culms or shoots were then detached, and an area-equivalent under a 0,6cm diameter cork borer was removed and placed in a scintillation vial. 0,2ml 50% perchloric acid and 0,4 mls 30% H_2O_2 were added, and the vials left open in an oven at 75°C for an hour, for all the substrate to dissolve.5 mls scintillation cocktail (Dimilume® - 30) was added and the vials left standing overnight in the scintillation counter. The samples were then counted for 20 minutes on a Beckman LS - 150 liquid scintillation counter.

There were three replicates per treatment, and 'blanks' consisted of vials containing reagents but no radioactive shoot/culm. Results were corrected using equation (1).

$$\text{C fixing efficiency} = \frac{\text{sample counts} - \text{blank counts}}{\text{area} \times (\text{exposure time to } ^{14}CO_2)} \times \frac{100}{\%ce} \qquad (1)$$

ce = counting efficiency

units = dpm (degradations min^{-1}) cm^{-2} min exposure $^{-1}$

3. RESULTS

3.1. Results

Table 3: pH and percent organic matter content at immature and mature stands.

SITE	pH	% ORGANIC MATTER (0-5cm)
Immature Stand	4,4	1,98
Mature Stand	4,0	4,31

Table 4: Changes in total and 'plant available' phosphorus at immature stand.*

Time	'Plant available' phosphorus	Total phosphorus
	μg P g^{-1} air dried soil (average 4 replicates)	μg P g^{-1} air dried soil (average 4 replicates)
Before burn	7,23 $\pm$ 0,06	34,85 $\pm$ 1,34
3 months after burn	4,40 $\pm$ 0,22	22,72 $\pm$ 0,75
6 months after burn	0,27 $\pm$ 0,05	16,15 $\pm$ 0,74
1 year after burn	1,74 $\pm$ 0,10	21,29 $\pm$ 1,29

* Data kindly provided by S. Jongens (see Appendix).

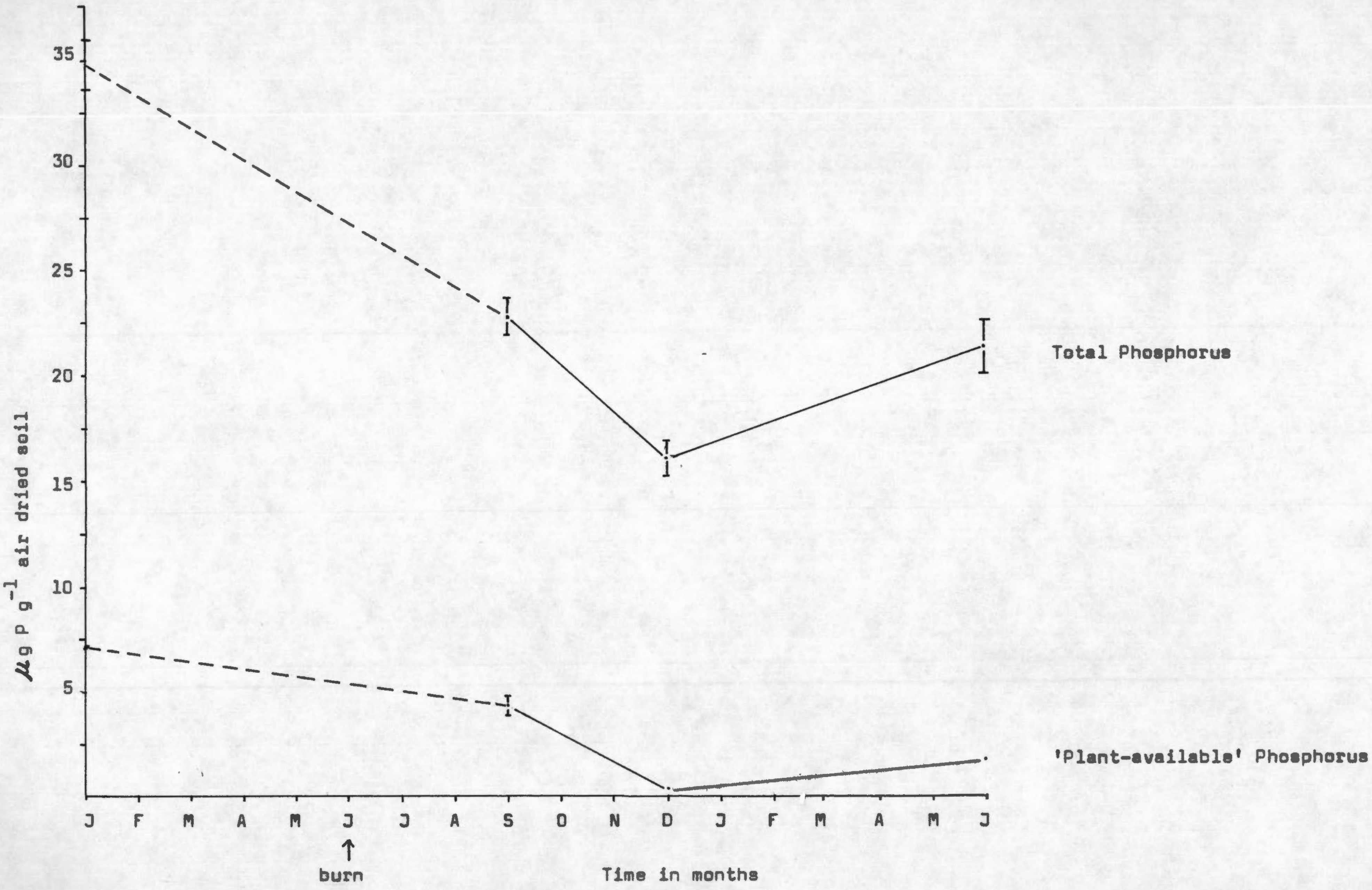

Figure 3: Change in total and plant available P at immature stand (1978/79)

Table 5: Relative photosynthetic rate determination, as measured by exposing plants to $^{14}CO_2$ for varying time periods

Stage of development *	Time of exposure to $^{14}CO_2$		
	10 mins	25 mins	45 mins
I	15,32 ± 11,42 dpm / cm^2 / min exposure	3,19 ± 0,69 dpm / cm^2 / min exposure	6,22 ± 3,56 dpm / cm^2 / min exposure
II - shoots	10,73 ± 10,96 dpm / cm^2 / min exposure	6,91 ± 3,78 dpm / cm^2 / min exposure	10,55 ± 13,26 dpm / cm^2 / min exposure
II - culms	19,64 ± 11,67 dpm / cm^2 / min exposure	14,98 ± 14,04 dpm / cm^2 / min exposure	1,42 ± 0,97 dpm / cm^2 / min exposure
III	219,91 ± 31,01 dpm / cm^2 / min exposure	199,11 ± 44,29 dpm / cm^2 / min exposure	202,73 ± 20,61 dpm / cm^2 / min exposure

(see Appendix)

* The stages were denoted subjectively on the basis of the ratio of shoot : culm growth. Stage I was predominantly shoot growth present in a bushy clump; Stage II culm and shoot growth roughly proportionate with some culms reproductive; Stage III was predominantly culm growth - almost all reproductive with still perhaps some bushy shoot growth present, though much would have died-back. Shoot-growth is also present here off the culms.

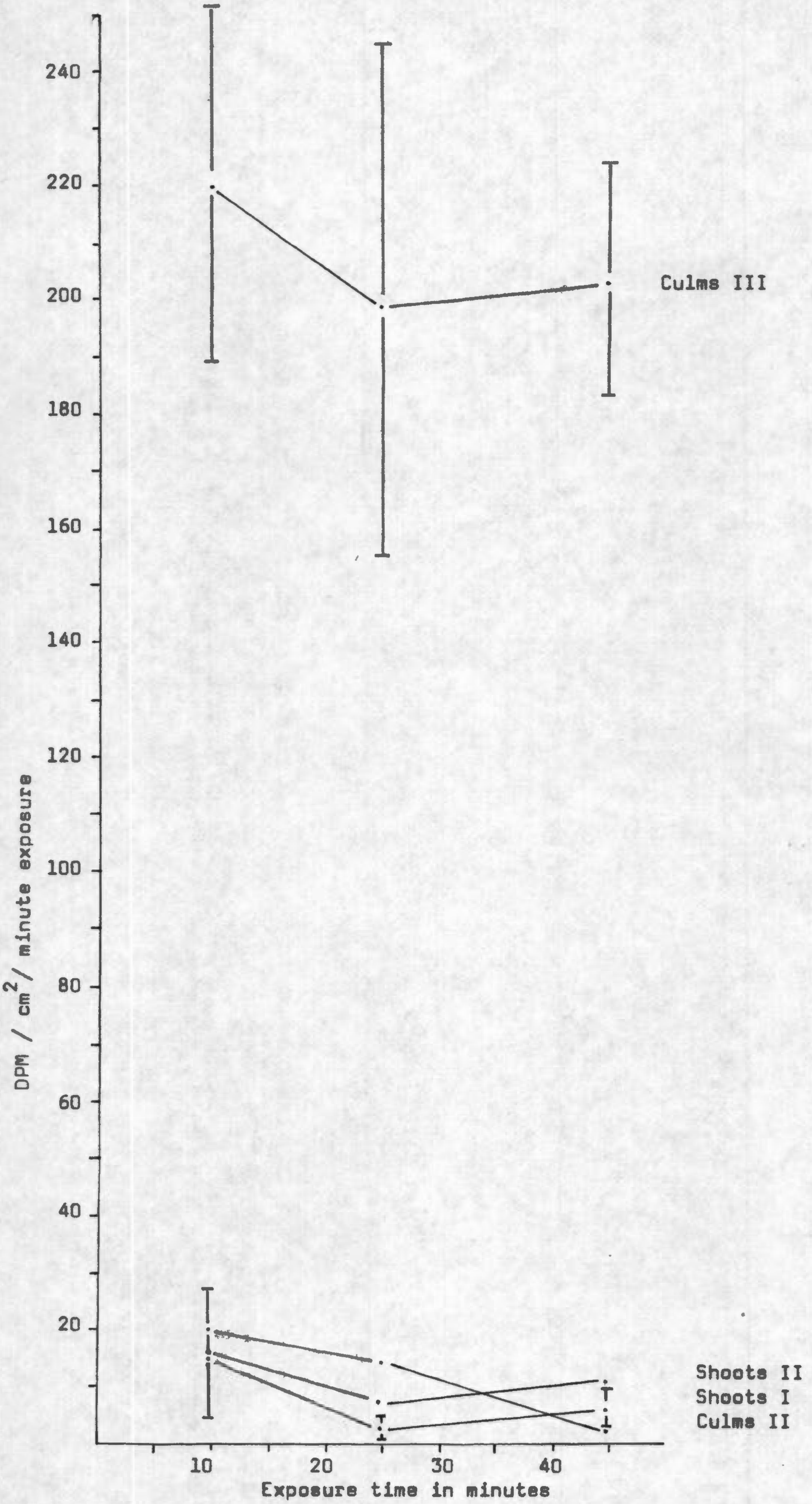

Figure 4: Relative photosynthetic rate after varying exposure time to $^{14}CO_2$

Tables 6 - 15: Description of study plants subjected to varying treatments of fertilization and phytomass removal.

Tables 6 - 9: Immature Stand.

Table 6: Treatment: Culm growth removed - no fertilizer	
General appearance:	plants healthy - but some yellowing at tips. In one case there was some die-back of shoots.
Culms:	in all cases new culm production was more prolific than cf. treatment date; height averaged between 15 and 20 cm. Dry weight production averaged between 6 and 20 g - depending on number and height of culms.
Shoots:	in all cases shoot height averaged at approximately 10 cm shoots from compact 'bush' in which culm growth occurs.

Table 7: Treatment: Culm growth removed - fertilized	
General appearance:	plants yellowish in some cases about 10% dead shoot growth present in the centre of the clump - fertilizer granules present.
Culms:	in all cases, new culm production was slightly more prolific cf. treatment date; height averaged between 15 and 25 cm. Dry weight production averaged between 3 and 11 g - depending on number and height of culms.
Shoots:	in all cases, shoot height averaged at approximately 11 cm.

Table 8: Entire plant clipped to ground - no fertilizer.
General appearance: plants healthy and green. Plant in replicate site had no culms.
Culms: new culm production in the plant at the original plot was more prolific cf treatment date. Height was approximately 8 cm, and dry weight 1,75g.
Shoots: shoot height at original plot 3 cm; while at replicate site it was 6,5 cm.

Table 9: Treatment: Entire plant clipped to ground - fertilized.
General appearance: plants healthy and green.
Culms: one plant in each site had only one culm, while other plants subjected to this treatment had slighter more prolific culm growth cf. treatment date. Height was approximately 8 - 14,5 cm; dry weight 0,16 g (1 culm) to 3 g.
Shoots: shoot height was approximately 7 cm, except at the plant with the most prolific culm growth, where it was 3 cm.

Tables 10 - 15: Mature Stand.

Table 10: Treatment: Culms cut to 10 cm height - No fertilizer.
General appearance: Plants healthy. Generally very little or no new shoot growth, mainly new culm production. Some cut culms died, others had shoots arising near cut surface.
Culms: Number of new culms produced varied from 4 - 24. Height varied from 10 cm - 25 cm.
Shoots: Plant with new shoot growth had approximately 8 shoots of height 9 cm. Shoot growth already existing at commencement of treatment 12 cm high. Shoot growth at cut surfaces occurs at 10 cm height.

Table 11: Treatment: Culms cut to 10 cm height - fertilized.
General appearance: Plants healthy. Generally very little - no new shoot growth; mainly new culms produced. Some cut culms died, other cut culms had shoot growth near cut surface. Shoot growth around perimeter of some plants shows extensive die back.
Culms: Number new culms produced varied from 12 - 43. Height varied from 18 - 37 cm.
Shoots: 2 plants with new shoot growth had approximately 4 shoots of height 9 cm. Shoot growth already existing at commencement of treatment approximately 10 cm high. Shoot growth at cut surfaces occurs at 10 cm height.

Table 12:	Treatment: Entire plant clipped to ground - no fertilizer.
General appearance:	Plants healthy. Mainly culm growth produced. Some new shoot growth at one plant.
Culms:	Number produced varied from 1 - 18. Height 10 cm - 16 cm.
Shoots:	Plant with shoot growth had 6 new shoots at height 3 cm. On a few culms some shoot growth at approximately 10 cm height.

Table 13:	Treatment: Entire plant clipped to ground - fertilized.
General appearance:	Mainly culm growth produced. One plant suffered die-back and only 2 shoots surviving.
Culms:	Number produced varied from 0 - 30. Height ranged from 14 - 22 cm.
Shoots:	Height varied from 3 - 10 cm. Some shoot growth arose new, other from cut surfaces of clipped culms.

Table 14:	Treatment: Entire plant clipped to 1 cm below ground level - no fertilizer.
General appearance:	Mainly culm growth produced overall. Plants healthy.
Culms:	Number culms produced varied from 1 - 7. Heights varied from 7 - 20 cm high.
Shoots:	Shoot height averaged approximately 7 cm. Most shoots arose new, some from cut surfaces. 5 culms had shoot growth.

Table 15:	Treatment: Entire plant clipped to 1 cm below ground level - Fertilized.
General appearance:	One plant died. Mainly shoot growth on remaining plants.
Culms:	Number culms produced varies from 5 - 10; Height 6 - 12 cm.
Shoots:	New shoot growth approximately 6 - 10 cm high. Shoot growth from cut culm surfaces 3 cm high. Some shoot growth on culms at approximately 10 cm height.

3. RESULTS

In Table 3 the percent organic matter and average pH values are shown for each study site. The results presented for the organic matter are comparable to those derived for other study areas (see Kuyler, 1977 unpub.). Erosion could be the factor accounting for the low value at the mature plot, while the significantly lower value at the immature site may be associated with the sparser vegetation cover.

The pH values indicate the soil is typical of that generally associated with the fynbos vegetation, being an acidic sandstone-derived soil (Cowling, 1978 unpub.). These features are also usually correlated with low nutrient status - especially with respect to nitrogen and phosphorus levels (du Toit, 1954). The phosphorus levels determined at the immature site are presented in Table 4 and Figure 3, and it is apparent that the amount of phosphorus available to the plants is only a fraction of that actually present. The sharp decrease in concentration between September and December 1978 (three and six months following the burn) may be correlated with re-growth of the vegetation. With the formation of some litter and the slowing down of growth in winter, phosphorus levels may be expected to rise slightly, as is illustrated by the increased value obtained in June 1979.

Unfortunately, phosphorus concentration was not determined immediately after the fire, but a previous worker (Kuyler, 1977 unpub.) has sbown that there is a post-burn increase in phosphorus concentration in the soil (see also Specht et al, 1958).

Table 5 and Figure 4 show relative photosynthetic rate as determined for the various 'successionary' stages of the species under investigation. Relative rates are plotted against exposure time to $^{14}CO_2$. The decrease in radioactivity with exposure time is probably due to the translocation

of / -

of photosynthates away from the irradiated area, and the slight increase in radioactivity observed at 45 minutes could result from a minor build up of photosynthates. It is felt however, that the initial exposure period was too long, and perhaps a better reflection of the photosynthetic rate would have been obtained with an additional exposure of only 2 - 3 minutes.

The culms showed higher photosynthetic rates compared with the shoots, but the difference was significant only between the third and first stages. The value obtained for the stage III culms may be a reflection of either (a) a higher photosynthetic rate or (b) a low photosynthetic rate and translocation rate, resulting in an accumulation of radioactivity.

The effects of phytomass removal and nutrient addition on the experimental plants are presented in Tables 6 - 15. As this project was a preliminary investigation, the majority of the results presented are descriptive.

The plants were examined for re-growth at monthly intervals, and those plants surviving the treatment were found to commence their re-growth within 1 - 1½ months, with the mature site plants recovering slightly faster. Growth rate was more rapid once the rains arrived. These results appear to be comparable with those obtained by Purdie (1977) in Australia, in an investigation into the early stages of regeneration after burning.

The fertilizer treatment appeared to have no consistent effect in favouring production of either culms or shoots, or in affecting growth rates within or between the plots. The rate and/or amount of fertilizer applied proved to be too high, since most of the fertilized plants had, at some stage, granules remaining at the time of a subsequent application. However, the possible detrimental effects of over-application could have been reduced by rain wash.

4. DISCUSSION

As mentioned in the introduction, the hypothesis proposed originally in this investigation was that phytomass removal would stimulate shoot development, and with the increased nutrient availability rapid growth to the bushy form could ensue. Maximization of the resources could be obtained if the shoots were efficient photosynthesizers, and energy could be channelled into repairs and the development of the reproductive structures - the culms. Thus the bushy shoot growth was postulated as being an adaptive mechanism contributing to the survival of these plants in a region subjected to fairly frequent fires.

However, in this study the proposed sequence of recovery was not apparent. Although in a few cases removal of the above ground parts and fertilization resulted in bushy shoot development prior to culm growth, the results obtained were inconsistent. In general, culm growth predominated, irrespective of whether nutrients were supplied or not.

Shoot initiation appears to be stimulated by damage, as shoot growth was almost always present on the experimental plants, irrespective of the height at which the damage was performed. The resprouting occurred near the cut culm surface. Figure 5 illustrates the shoot growth present off the culms cut to a height of 10 cm. That this feature also occurs following a burn was demonstrated by examining another *Thamnochortus punctatus* plant at the immature site, and arising off the burnt culm was shoot growth (Figure 6).

The rapid re-growth of the culms apparent in this investigation may be an anomalous result, as only damage and additional nutrient effects were investigated - heat injury however was not taken into account. Monthly rate of recovery, and in some cases total recovery of species, is influenced most by the extent of heat injury received by the plants (Purdie, 1977).

If heat injury affects the culms more than the shoots, then following a fire damage would stimulate the development of shoots, and then only later would culm re-growth occur. The plants in the mature and immature stand did not differ in their responses to treatment, but other investigators have demonstrated that both shoot initiation and tolerance to heat stress tend to decrease with plant age (Blaisdell and Mueggler, 1956; Whittaker and Gimmingham, 1962; Biswell, 1974).

Another possibility is that the results may have been influenced by the timing of this investigation. The study was conducted predominantly through the winter, and recovery may be influenced by carbohydrate reserves (Mooney and Dunn, 1970), as fynbos has a summer growth rhythm (Levyns, 1964). In addition, moisture is readily available in winter (a characteristic of mediterranean typé climates), and Purdie (1977) found that initiation of shoot development was governed by moisture availability. If this study was repeated in the dry summer, culm production could possibly be delayed, as the damage would stimulate shoot growth and available water may be utilized by the shoots in their growth, and development of some reserves, with culm growth only being initiated later.

The timing may also have influenced the observed photosynthetic rates. Previous work on <u>Thamnochortus</u> photosynthesis was performed by Professor Cresswell (Moll, pers. comm.) in the mid-summer (February) of 1977. The unpublished data indicated that the culms had a considerably lower photosynthetic rate when compared to the shoots. The data obtained in the two studies are not directly comparable however, in terms of the units of measurement employed; and in prior environmental conditions experienced in the field, which Slayter and Morrow (1977) have demonstrated may influence the results.

The culms and shoots of stages I and II had approximately the same relative photosynthetic rates. The high rate observed for the culms at stage III,

Figure 5: Shoot growth of culm cut to height 10 cm
Shoot growth occurred following damage.

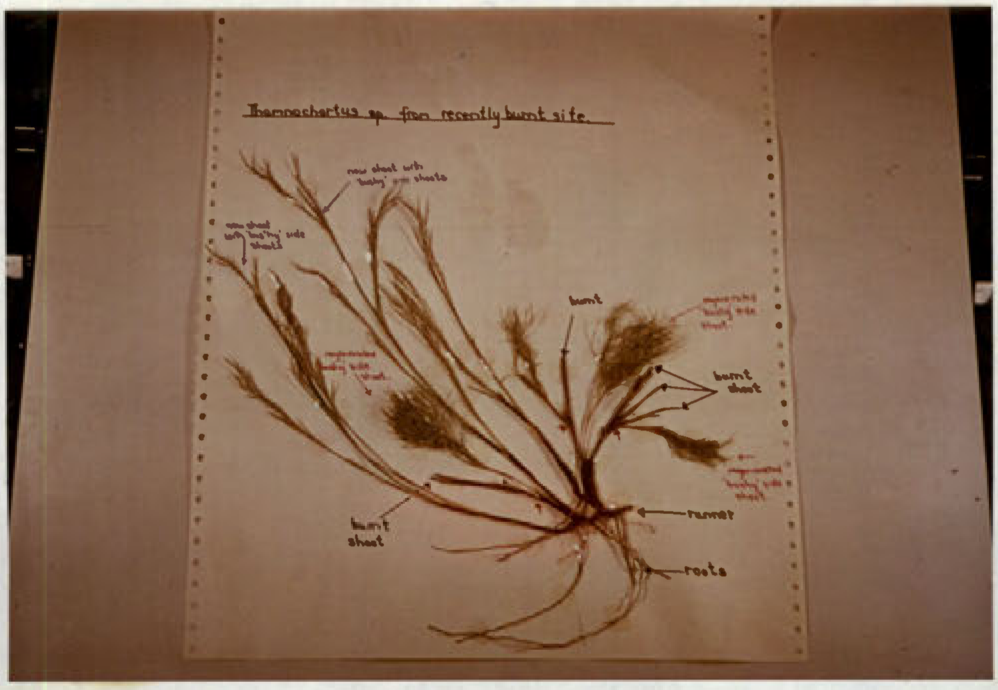

Figure 6: Thamnochortus punctatas plant from immature site, showing bushy shoot growth of burnt culms.

could be correlated to their reproductive status, and this ties in with the point raised earlier, that the result could be due to an accumulation of radioactivity near the inflorescence.

It may therefore be suggested that if moisture and carbohydrate reserves are available, and the plant is not subjected to heat injury, then culm regrowth can be initiated almost immediately. Damage stimulates shoot growth, so these structures will be present but will not predominate. Consequently the results obtained in this investigation cannot be considered as reflecting the changes experienced following a burn.

5. CONCLUSIONS AND SUGGESTIONS FOR FURTHER WORK

It was suggested from field observations that shoot growth may provide a more effective means of sprouting following a burn. This sprouting may be of possible survival value if it allows the plant a means of rapid regeneration, enabling available nutrients and moisture to be utilized while competion is still reduced.

Though the results obtained in this preliminary investigation do not appear to substantiate the observed recovery of plants in the field, it is felt that this is due to the omission of heat injury as an important post-fire effect. It is suggested that resistance to heat injury may vary within the plant in relation to the production of shoots or culms, and between plants as a consequence of age. Timing of the study may influence the availability of moisture, and reserves accumulated from the growth season. Photosynthetic rate may vary seasonlly and with the reproductive status of the plant, so timing is an important consideration here as well.

It is felt that further work should be carried out on this interesting phenomenon of the post-burn bushy shoot stage, and the principal areas of research should concentrate on an investigation of the phenology of the species, incorporating seasonal relative photosynthetic rate and possible carbohydrate translocations. Since fertilization (not the right term) does not have any marked influence on regrowth, it is felt that this treatment should be discarded, and the effects of heat stress damage investigated.

ACKNOWLEDGEMENTS

I would like to thank my project supervisor Dr. Eugene Moll, for his encouragement and assistance throughout. Dr. Sharon Jongens kindly provided the data on phosphorus concentrations at the immature stand, and Professor R. Specht made highly valued comments and suggestions.

Ms Sonia Rondot provided invaluable assistance in the field and unfailing encouragement during more sober periods; chores beyond mere thanks. Mrs. E. Strickland kindly typed the final document.

REFERENCES:

ACOCKS, J.P.H. 1953 - Veld types of S.A. Mem. Bot. Surv. S. Af. 18 : 128 pp. (2nd Ed. 1975).

BISWELL, H.H. 1974 - Effects of fire on chaparral. In Fire and Ecosystems; ed. T.T. Kozlowski and C.E. Ahlgren pp. 321 - 64. Academic Press, New York.

BLAISDELL, J.P. and MUEGGLER, W.F. 1956 - Sprouting of bitterbush (Purshia tridentata) following burning or top removal. Eco. 37 : 365 - 70.

CHRISTENSEN, N.L. 1973 - Fire and the nitrogen cycle in California Chaparral. Science 181 : 66 - 68.

COWLING, R. 1978 (unpub.) Evolution and diversification in the Cape flora. Seminar - Botany Hons. U.C.T.

DEBANO, L.F. and CONRAD, C.E. 1974 - Effect of wetting agent and nitrogen fertilizer on establishment of ryegrass and mustard on a burned watershed. J. Range Management 27 : 57 - 60.

DEBANO, L.F. and CONRAD, C.E. 1978 - The effect of fire on nutrients in a chaparral ecosystem. Eco. 59(3) : 489 - 97.

DOBZHANSKY, T. 1956 - What is an adaptive trait? Am. Nat. 90 : 337 - 47.

DU TOIT, A.L. 1954 - The Geology of S.A. 3rd Ed. Oliver and Boyd, Edinburgh.

GILL, A.M. 1975 - Fire and the Australian flora : A Review. Aust. For. 38 : 4 - 25.

________ 1978 - Plant traits adaptive to fires in Mediterranean land ecosystems. In Mooney, H.A. and Conrad, C.E. (eds.) p. - 26. Proc. of Symp. on Fire & Fuel Management in Medit. ecosystems. U.S.D.A. Forest Service. Gen. Tech. Rep. Wo - 3.

GILL, A.M. and GROVES, R.H. 1979 - Fire regimes in heathlands and their plant-ecological effects. In Specht, R.L. (ed.). Heathlands of the World (in press).

GRIER, C.C. 1975 - Wildfire effects on nutrient distribution and leaching in coniferous ecosystem. Can. J. For. Res. 5(4) : 599 - 607.

HANES, T.L. 1977 - California chaparral. In Terrestrial vegetation of California. Barbour, M.G. and Major, T. (ed.). p. 417 - 470. John Wiley & Sons, Inc.

HESS, P.R. 1971 - Textbook of soil chemical analysis. John Murray, London.

KRUGER, F.J. 1977 - Ecology of the Cape fynbos in relation to fire. In Mooney, H.A. and Conrad, C.E. (eds.). p. 230 - 244 (op. cit).

KUYLER, P. 1977 - (unpub). A study of the relationship between soil and litter nutrient status and fire in the fynbos ecosystem. Botany Hons. project, U.C.T.

LEVYNS, M.R. 1964 - Migrations and origins of the Cape Flora. Trans. Roy. Soc. S.Af. 37(2) : 85 - 107.

MOONEY, H.A. and DUNN, E.L. 1970 - Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. Evoln. 24 : 292 - 303.

MURPHY, J. and RILEY, J.P. 1962 - A modified single solution method for the determination of phosphate in natural waters. Anal. Chem. Acta. 27 : 31 - 36.

PARSONS, R. 1978 - (unpub). An investigation of the effect of fungal factors with variable sowing densities, on the mortality and performance of cress-seedlings. Third yr. project, Botany Dept. U.C.T.

PURDIE, R.W. 1977 - Early stages of regeneration after burning in dry sclerophyll vegetation. I Regeneration of the understorey by vegetative means. Aust. J. Bot. 25 : 21 - 34.

SLAYTER, R.O. and MORROW, P.A. - Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng I. Seasonal changes under field conditions in the snowy mountains area of south-eastern Australia. Aust. J. Bot. 25(1) : 1 - 20.

SPECHT, R.L., RAYSON, P. and JACKMAN, M.E. 1958 - Dark Island heath (Ninety-Mile Plain, South Australia VI. Pyric succession : Changes in composition, coverage, dry weight, and mineral nutrient status. Aust. J. Bot. 6 : 59 - 88.

TAYLOR, H.C. 1977 - The Cape floral kingdom, an ecological view. Proc. 2nd annual weeds conf. S.A. p. 19 - 33. Balkema Press, C.T.

TAYLOR, H.C. 1978 - Capensis. In M.J.A. Werger (ed.) Biogeography and ecology of S.A. Junk, The Hague : 171-229.

VOSNESENSKII, V.L., ZALENSKII, O.V. and AUSTIN, R.B. 1971 - Methods of measuring rates of photosynthesis using $^{14}CO_2$. In : Sestak, Z, Catský, J. and Jarvis, P.G. (Eds.) p. 276 - 93. Plant Photosynthetic Production - Manual of methods. Junk: The Hague.

WHITTAKER, R.H. and GIMMINGHAM, C.H. 1962 - The effects of fire on regeneration of *Calluna vulgaris* (L.) Hill from seed. J. Eco. 50 : 815 - 22.

APPENDIX

CHANGES IN TOTAL AND 'PLANT AVAILABLE' PHOSPHORUS AT IMMATURE STAND

Sample (4 replicates)	Bray # 2 g P g^{-1} air dried soil		Total Phosphorus μg P g^{-1} air dried soil	
	Replicates	Mean ± S.E.M.	Replicates	Mean ± S.E.M.
Before burn	7,37		33,28	
	7,26	7,23 ± 0,06	38,65	34,85 ± 1,34
	7,17		32,68	
	7,11		34,81	
After burn	3,80		24,86	22,72 ± 0,75
3 months	4,67	4,40 ± 0,22	20,76	
	4,34		23,17	
	4,77		22,10	
After burn	0,30		18,56	
6 months	0,18	0,27 ± 0,05	15,67	16,15 ± 0,74
	0,20		15,82	
	0,39		14,55	
After burn	1,44		20,77	
1 year	1,77	1,74 ± 0,10	25,07	21,29 ± 1,29
	1,89		20,04	
	1,84		19,30	

(Data kindly provided by S. Jongens).

APPENDIX

RELATIVE PHOTOSYNTHETIC RATE DETERMINATION

STAGE I : ALL SHOOTS

BLANK 92,75 cpm

Exposure Time	External Standard	% counting efficiency	cpm	cpm blank	cpm/cm^2	cpm/cm^2/ min. exposure	DPM	Average ± S.D.
10 mins.	0,176	78,0	155,7	62,95	222,44	22,24	28,51	
	0,178	78,5	112,2	19,45	68,73	6,87	,75	15,32±
	0,284	85,0	113,7	20,95	74,03	7,40	8,70	11,42
25 mins.	0,154	76,5	152,3	59,55	210,42	8,42	11,0	
	0,143	ND	70,8	-	-	-	-	3,19±
	0,221	81,0	139,2	46,45	164,13	6,57	8,10	0,69
	0,094	ND	72,6	-	-	-	-	
45 mins.	0,079	68,5	175,9	83,15	293,82	6,53	9,5	6,22±
	0,151	76,0	108,3	15,55	54,95	1,22	1,6	3,56
	0,146	ND	90,0	-	-	-	-	
	0,218	81,0	170,3	77,55	274,03	6,09	7,5	
	0,241	82,7	290,0	197,25	696,99	15,488	18,73	
	0,161	ND	92,4	-	-	-	-	

STAGE II : SHOOTS

BLANK 65,0 cpm

Exposure Time	External Standard	% counting efficiency	cpm	cpm blank	cpm/cm^2	cpm/cm^2/ min. exposure	DPM	Average ± S.D.
10 mins.	0,242	82,8	149,3	84,3	297,88	29,79	35,98	10,73±
	0,157	77,9	113,4	48,4	171,02	17,10	21,95	10,96
	0,173	78,0	71,0	6,0	21,20	2,12	2,71	
	0,259	84,0	61,8	-	-	-	-	
	0,246	83,0	108,4	43,4	153,36	15,34	18,48	
	0,340	88,0	72,4	7,4	26,15	2,62	2,98	
25 mins.	0,277	83,5	90,0	25,0	88,34	3,53	4,23	
	0,291	86,5	57,3	-	-	-	-	6,91±
	0,372	90,0	126,0	61,0	215,55	8,62	9,58	3,78

45 mins.	0,097	71,0	53,7	–	–	–	–	
	0,283	85,0	266,3	201,3	711,31	15,81	18,6	10,55±
	0,125	74,0	169,7	104,7	369,96	8,22	11,11	13,26
	0,325	87,5	281,4	216,4	764,66	16,99	19,42	
	0,279	85,0	49,8	–	–	–	–	
	0,386	90,5	84,2	19,2	67,84	1,51	1,67	

STAGE II : CULMS
BLANK 50,2 cpm

Exposure Time	External Standard	% counting efficiency	cpm	cpm blank	cpm/cm^2	cpm/cm^2/ min. exposure	DPM	Average ± S.D.
10 mins.	0,293	85,5	129,5	79,3	280,2	28,02	32,77	19,64±
	0,282	85,0	88,0	37,8	133,57	13,36	15,72	11,67
	0,218	81,0	74,1	23,9	84,45	8,45	10,43	
25 mins.	0,209	80,5	85,4	35,2	124,38	4,98	6,19	
	0,251	83,0	94,7	44,5	157,24	6,29	7,58	14,98±
	0,265	84,0	235,5	185,3	154,77	26,19	31,18	14,04
45 mins.	0,231	82,0	89,9	39,7	66,16	1,47	1,79	1,42±
	0,268	84,0	64,4	14,2	50,18	1,12	1,13	0,97
	0,214	81,0	82,5	32,3	114,13	2,54	3,14	

STAGE III : ALL CULMS
BLANK 126,7

Exposure Time	External Standard	% counting efficiency	cpm	cpm blank	cpm/cm^2	cpm/cm^2/ min. exposure	DPM	Average ± S.D.
10 mins.	0,283	85,0	698,8	572,1	2021,55	202,16	237,83	219,91
	0,323	87,0	712,2	585,5	2068,9	206,89	238,80	
	0,335	88,0	585,2	458,5	1620,14	162,01	184,10	
25 mins.	0,330	88,0	1544,2	1417,5	5008,83	200,35	227,67	±
	0,306	86,5	1482,7	1356,0	4791,5	191,66	221,67	199,11
	0,185	79,0	954,4	827,7	2924,73	116,99	148,09	44,29
45 mins.	0,198	80,0	2370,5	2243,8	7928,6	176,19	220,24	±
	0,204	80,0	2245,2	2118,5	7485,87	166,35	207,94	202,73
	0,208	85,0	2075,4	1948,7	6885,87	153,02	180,02	20,61

ND : Not Determined.