USE OF THESES

INVASION OF COASTAL ACACIA

COMMUNITIES BY CHRYSANTHEMOIDES

by

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"Small herbs have grace, great weeds do grow apace:
And since, methinks, I would not grow so fast,
Because sweet flowers are slow, and weeds make haste."
(Shakespeare 1790)

Part of the main study site at South Beach, Moruya, N.S.W. showing invasion by <u>Chrysanthemoides</u> <u>monilifera</u> ssp. <u>rotundata</u> on the mid-dune (foreground) and on the fore-dune (background). <u>Acacia</u> <u>longifolia</u> var. <u>sophorae</u> and the taller species, <u>Banksia</u> <u>integrifolia</u> can also be seen on the fore-dune.

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Statement of originality

This research is entirely my own work except for the surveys reported in Chapter 1 and the burning control program in Chapter 10.

The survey data on the North Coast was contributed by the National Parks and Wildlife Service of N.S.W. and that on the South Coast obtained jointly by me and the above organisation.

Planning of the burning program was done largely by me but Dr. Rosemary Purdie was responsible for most of its implementation.

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ABSTRACT

Many of the disturbed coastal sand-dune communities in New South Wales are being invaded by the South African shrub, Chrysanthemoides monilifera ssp. rotundata (boneseed, bitou bush). In some stands, this has resulted in displacement of the previous dominant, Acacia longifolia var. sophorae (coastal wattle). In South Africa, closely related Acacia ssp. are invasive, so a study of both Chrysanthemoides and Acacia provided a means of better understanding the invasion process.

The main factors in the success of Chrysanthemoides in Australia are flowering mainly from autumn to spring, a yearly output of over 4000 seeds m^{-2}, efficient dispersal particularly by birds, and low predation. Acacia flowers only in spring and produces c. 100 seeds m^{-2}, which are poorly dispersed and highly predated. Although remaining Acacia seeds have greater longevity in the soil than Chrysanthemoides, in established stands there are c. 60 times more viable Chrysanthemoides seeds in the soil than Acacia. By contrast in South Africa, lower predation of the Australian species results in up to 50 times more Acacia seeds than of the native Chrysanthemoides.

In unburnt areas in Australia, there were 500 times more seedlings of Chrysanthemoides than Acacia. Differences in seedling strategies were apparent in that Chrysanthemoides was able to avoid water stress to some extent by rapid root development and early closure of stomates as leaf water potential dropped. By contrast, Acacia was more typical of Australian sclerophylls and was able to tolerate lower leaf water potentials and, under even severe water stress, had low mortality except in mixtures where the greater transpiration of Chrysanthemoides resulted in similar mortality of both species. Chrysanthemoides outcompeted Acacia in terms of biomass when well-watered but not under water stress.

Under controlled conditions, the potential invasiveness of Acacia was demonstrated in its having the higher rate of CO_2 assimilation per unit leaf area but both species had similar rates in the field and Chrysanthemoides had the greater leaf area.

Regenerative strategies of the two species after fire also differed. In unburnt areas, there was a bank of persistent, slow-growing seedlings of Chrysanthemoides but very few seedlings of

Acacia or other native /species. Fire killed adult Acacias but enhanced germination which resulted in a 13-fold increase in subsequent seedling density. By contrast, 26% of adult Chrysanthemoides resprouted and while .30% of seeds were killed, subsequent Chrysanthemoides seedlings' still outnumbered those of Acacia by some 20 times. Seedlings of both species responded by greater growth rates in burnt areas but Chrysanthemoides was more precocious in that flowering and seeding occurred within 12 months of emergence.

Measures to control Chrysanthemoides by a program of double-burning were successful in limiting resprouting to 5% or less of plants but a problem still remained of seedlings which emerged from deeply buried seeds. Thus other measures such as biological control for which there is ample potential need to be assessed.

Chapter 1

Introduction

"Studies of ecosystems on this planet can be neither complete nor valid unless they take account of the pervasive and sometimes overwhelming role played by man's activities."
(Aschmann 1973)

"If all the introduced fauna (including man) were removed the evidence strongly favours the view that the aliens would be conquered by the indigenes, surviving only in greatly reduced numbers and as very subordinate members of the resulting ecosystem."
(Allan 1936)

"The impact of white man on the Australian environment in 200 years has been profound. He has so modified the landscape that every habitat has been changed in some way by introduced animals, plants and micro-organisms."
(Fox & Adamson 1979).

Most of Australia's horticultural and agricultural plants are included in the 1500 exotic species of flowering plants which have become naturalized in Australia (Wace 1973). Also included, however, are some accidental as well as deliberate introductions that have escaped the confines of domestication. Indeed, ten of the species recommended by the first Government Botanist for introduction to Victoria (Von Mueller 1888) are now serious weeds proclaimed noxious by law in that State. The success of weeds as colonisers of large areas of Australia can be seen from the fact that there is an average of 57 weeds proclaimed in each State (Amor & Twentyman 1974). The number of potential candidates is also increasing, since Amor & Piggin (1977) estimate that in Victoria there is an increase of six naturalized species per year.

1.1 Definitions

The definition of a weed has depended on one's reasons for wanting such a definition. For example, a weed has been often defined as "a plant growing out of place" or "a plant in the wrong place" (Bunting 1960). Such descriptions place a value judgment on the plant as something undesirable or unwanted from man's point of view. The above definition has been reversed to "a plant growing in place" (Parsons 1973) which implies the plant's point of view as being the more important. In other words, the plant has become successful and a weed in a particular area because of the favourable environment that it encounters there. However, this definition is of little use as it could also apply to many species in natural ecosystems which are not considered as weeds. For example, grazing and clearing of Acacia pendula (weeping myall) and Atriplex nummularia (oldman saltbush) on the eastern Riverine plain of New South Wales has led to their almost local extinction, resulting in the grasses Danthonia sp. and Chloris sp. becoming much more numerous (Moore 1962; Williams 1962). Yet the success of these species under grazing has not led to their being regarded as weeds.

Later definitions have considered both the importance of a suitable environment for the plant and man's influence in creating that environment. For example, a plant may be a weed "if in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man" (Baker 1974).

Again, "weeds are plants which grow entirely or predominantly in disturbed areas, and they produce large numbers of seeds adapted to long distance dispersal by wind or by animals" (Krebs 1978). However, these definitions do not emphasise the inherent undesirability of the plant which may vary in different areas. For example, Paspalum dilatatum may be valuable as a pasture species but undesirable as a component of a domestic lawn. This point is brought out in the dictionary definition of a weed as a "wild herb growing where it is not wanted" (Anon. 1964).

Another objection to the above definitions is that disturbance is not a pre-requisite for a suitable environment for weed growth, as discussed later (Section 1.2), although weeds are more common in disturbed areas. Further, prolific seed production is not a necessary attribute as weeds such as Pteridium esculentum (bracken) and Eichhornia crassipes (water hyacinth) depend almost exclusively on vegetative reproduction.

The present study is concerned with "invasive" plants, i.e. those which, as defined in the Oxford Dictionary, "swarm into, encroach upon or make hostile inroads into a country" (Anon. 1964). Thus a better definition of a weed than those already cited may be: "a plant, usually an exotic, possessing characteristics which, when able to be realised in a particular environment, enable it to invade and persist in habitats where it may or may not displace any existing vegetation and becomes undesirable". Of course, there are degrees in this definition and so the degree of spread, length of persistence and amount of displacement of any existing vegetation determine whether a plant is considered a serious weed or one of lesser importance.

In the past, the term "invade" has been used rather loosely. For example, eleven Australian species (including six Acacias) have been classified as plant invaders in South Africa (Stirton 1978). However, Shaughnessy (1980) has been perhaps too rigorous in her definition of "invader" and has limited it to those species which "occur more widely now than when planted". If its distribution is similar now to that when it was planted, then it is classed as persistent but not invasive. Thirdly, if it is less widespread now than when planted, it is non-invasive.

Of the eleven species described as invaders by Stirton (1978) which were introduced into the Table Mountain region near Cape Town, Shaughnessy (1980), on the basis of the above definition, considered

only Acacia longifolia, Albizia lophantha and Hakea sericea as invasive. McLachlan, Moll & Hall (1980) found also that A. longifolia and H. sericea were two of the species that occurred more widely in the Cape Peninsula in 1976 than in 1959-60.

Some difficulties arise, however, when using the criteria of Shaughnessy to classify the invasiveness of a plant. For example, how far does a plant need to spread before it is invasive rather than persistent? In the present study, if a plant has been introduced into a particular area by whatever means (sowing by man, dispersal of seed by birds, water or wind) and has grown such that it has fulfilled the earlier definition of a weed, then it has been classed as invasive.

1.2 Reasons for the Study

Most studies of weeds have concentrated on agricultural systems (Gregory & Weiss 1963, 1965; Molnar & Donaldson 1970; Reeves & Tuohey 1970; Russell 1970; Wells 1970). However, in recent years, some attention has been paid to weeds of natural ecosystems. For example, a Victorian report (Anon. 1976) listed 24 weeds which pose a threat to native species in bushland. Of these weeds, only the South African species, Chrysanthemoides monilifera (boneseed) and Polygala myrtifolia (myrtle-leaf milkwort) can be considered weeds exclusively of natural as opposed to agricultural habitats.

The reason weeds have been less well studied in natural ecosystems compared with those in man-made ones as in agriculture is probably because it is easier to demonstrate economic losses by the individual farmer due to agricultural weeds. Consequently these attract more resources for study and so have received much greater attention (Amor & Piggin 1977).

However, natural ecosystems such as grazing lands with native pasture, forests, water-catchment areas and coastal sand dunes also represent areas which are economically very important from the point of view of maintaining their integrity to fulfill their intended role. The main difference from agricultural lands, however, is that the costs of maintaining these natural areas is a diffuse one which must be borne by governments and indirectly by all taxpayers. Besides the main effect of weeds in preventing efficient utilisation of these natural areas, there are also their effects on aesthetics, access and integrity of the native flora and associated fauna.

Recent studies on such weeds in Australia have included the invasion of Eucalyptus forest by Pinus radiata (Monterey pine) (Burdon & Chilvers 1977; Foster 1979), invasion of natural waterways by Eichhornia crassipes (water hyacinth) (Forno & Wright 1981), Alternanthera philoxeroides (alligator weed) (Julien & Broadbent 1980), Salvinia molesta (salvinia) (Harley & Mitchell 1981) and roadside invasions by Cinnamomum camphora (camphor laurel) (Firth 1979). Most, however, have concentrated on the autecology of invading species rather than the reasons for their success and the effect on the invaded community.

1.3 Reasons for invasion

Some possible reasons for invasion of natural communities are:

1. Predators so restrict the growth of some plant species in their native habitat, that these plants have evolved a high reproductive potential in order to survive. When these plant species are introduced into a particular area without their former predators, this reproductive potential enables them to increase their numbers in that area and, given adequate dispersal mechanisms, to spread to other areas.

This has been demonstrated with the Australian species Acacia longifolia which was introduced into South Africa where it produces large numbers of viable seeds and has there become a serious weed (Milton & Hall 1981). In these situations A. longifolia could be considered to be occupying a "realised niche" (that effective in the presence of competitors and predators) in Australia and at least closer to a "potential niche" (that effective in the absence of competitors and predators) in South Africa (Hutchinson 1957).

2. Another reason may be that there are some communities with empty niches which provide opportunities for colonisation and then expansion by a plant invader.

3. A third reason may be that some communities have weak species (either inherently so or because of predators) occupying certain niches. These plants suffer from competition when an invader also occupies that niche, causing displacement of the original plants.

1.4 Predisposition of a site to invasion

Not only is the biology of a weed an important factor in invasion by it but an answer to the question of what predisposes a site to invasion is necessary to fully understand the processes involved. The concept of invasion in relation to vegetational composition and species richness has been considered by several workers. Clements, Weaver & Hanson (1929) found that it was practically impossible to introduce Typha sp. (bulrush) into a Phragmites sp. (reed) community and vice versa. They concluded that modification or replacement of a climax association can only be brought about by mass migration aided by dramatic environmental change.

Harper (1965) found that the resistance of an established community to an invading exotic species was inversely proportional to the diversity of the community. On the other hand, Fosberg (1967) stated that in areas of low species richness or diversity, there are consequently unoccupied niches which are available to invading species. At the other extreme of high species richness, he considered that disturbance created new niches, which can similarly be occupied by exotics. It may thus be only communities of intermediate diversity which are resistant to invasion.

1.4.1 Site condition

Several reports have concentrated on the conditions necessary for successful invasion. For example, Sagar & Harper (1961) showed that grass removal was necessary for seedling establishment of three Plantago species, especially of those species not occurring naturally in the communities studied. Sagar (1960) found that seedlings of a species previously absent were not successful in establishing plants except in cultivated land. Juhren & Montgomery (1977) reported that Cistus seedlings invaded disturbed wildland sites in southern California only if not overtopped by tall chaparral and if thick grass was absent. Fenner (1978) sowed a range of species into small gaps in short and tall turf. Germination of ruderals was greatly reduced in tall turf and seedlings of both ruderals and closed turf species grew very poorly in tall turf.

Of various habitats into which three taxa of Rumex were introduced, the most successful establishment occurred in an uncolonised habitat (a new shingle site) (Cavers & Harper 1967). Habitats in which one or more of the taxa were abundant did not

permit further recruitment. Two alternatives were put forward to explain this:

(i)   The existing populations represented a relic from an earlier condition of the habitat when the environment was favourable for establishment.

(ii) The habitats chosen may have already reached saturation densities of <u>Rumex</u>.

Putwain & Harper (1970) also sowed <u>R. acetosa</u> and <u>R. acetosella</u> in swards treated with herbicides. <u>R. acetosa</u> spread rapidly after removal of grasses but increases in <u>R. acetosella</u> occurred only when both grasses and dicotyledonous species were removed.

Holt (1972) found that establishment of reproductive populations of <u>Daucus carota</u> in southern Michigan old fields, was most sensitive to events prior to seedling emergence of this species. Reductions in emergence and delays in reproduction were caused by the presence of perennial grasses.

Seed of the biennial species <u>Dipsacus sylvestris</u> (teasel) was introduced into eight different types of vegetation in order to understand its colonisation success (Werner 1977). This was achieved only in the absence of deep grass litter and dense living grass. Where these were present, there were low seed germination and high seedling mortality. In successful cases, the teasel rosette created an opening in the vegetation which could be colonised by teasel seedlings. There was high seedling mortality in a field with a shade canopy and an understorey of herbaceous dicotyledonous species. This habitat also delayed the reproductive phase but the number of seeds produced was similar to more rapidly growing plants in other habitats. Teasel was able to colonise areas where other plants were dissimilar to it in life-history characteristics (e.g. perennial grasses), even if there was some canopy shading. Successful invasion also occurred in areas where the plants were similar to teasel, but only if there was no canopy shading.

1.4.2 Disturbance

- It has been stated that introduced plants rarely establish in stable plant communities without prior disturbance and modification of the environment, and their abundance usually increases with increasing disturbance of the original plant community (Moore 1967). Certainly there are few areas in Australia not disturbed by man or his activities. These disturbances include fire, trampling, clearing,

road-making, mining or other engineering works and activities associated with agriculture. Fire, for example, opens up canopies and releases nutrients in the soil (Gill 1975). In agricultural areas, the introduction of exotic grazing animals and the use of fertilisers which increase soil fertility have been two important factors allowing the mediterranean regions of Australia to be invaded by alien plants (Specht 1973). There are numerous examples of such plants in Australia (Michael 1981).

Less common are species which invade comparatively undisturbed areas although such areas are still subject to "natural" disturbance. Agents involved include wind and water causing soil erosion, native fauna causing defoliation or death and lightning strikes resulting in fires. It is of interest to examine the reasons for success of invading species in these situations since the magnitude and frequency of these natural disturbances are generally far less than those that are caused by man and his domestic animals (Amor & Piggin 1977). However, man-made factors can intensify the effects of a natural disturbance, e.g. trampling as well as wind erosion on sand dunes.

Wace (1967) concluded that there were 12 "highly aggressive" alien plant species on the Tristan da Cunha Islands in situations in which there had been virtually no human disturbance or grazing by introduced animals. Rather, the disturbance that had occurred in these areas had been due to "natural" causes such as wind erosion in coastal habitats and landslips.

Other reports indicate that alien plants such as Hakea sericea (silky hakea) and Pinus pinaster (cluster pine) have invaded undisturbed fynbos in South Africa (Anon. 1967). Also it is claimed that C. monilifera can establish in Australia in "areas of native vegetation whether disturbed or not" (Parsons 1973). Another report (Anon. 1976) states that this same species has the ability to invade areas of "relatively little disturbance". However, the same report admits that there are "very few areas of undisturbed bushland in Victoria" and that "none of the national parks in Victoria has been able to escape some clearing, grazing or mining at some stage in its recent history".

Some authors have not distinguished between these various types of disturbances in relation to invasion. Thus Elton (1958) merely emphasised that disturbance "in some form" was a precursor of weed invasion. Again, Harper (1965) has stated that: "Almost inevitably an invading species becomes established in areas in which some other

disturbance has occurred, and both the entry of the alien and any reduction in the abundance of a native can usually be associated with the disturbance of the habitat". However, disturbance of the habitat, such as by fire or grazing, may induce vegetational changes without weed invasion. For example, Acacias are well known to increase in density after fire because of stimulation of seed germination (Luke & McArthur 1978).

In general, however, it appears that the more disturbed the habitat (by whatever means), the greater is the likelihood of successful weed invasion. In this context, it is relevant to this study to note that Australian mediterranean regions "may well be the world's most disturbed" while the mountain fynbos in South Africa is "perhaps the least modified in the world" (Aschmann 1973).

1.5 The process of invasion

The process of invasion of alien plants into native vegetation was apparently first described by J.D. Hooker and Charles Darwin over 100 years ago. Thus Hooker (1860) described the establishment of an exotic weed in an already vegetated situation, with the final result depending on "that power of appropriation (by the weed) in the strife for place which has not even a name in the language of biology". Even at this early date, less than 100 years after colonisation by Europeans, Hooker listed 139 naturalised plants in Australia.

Hooker also predicted that many of the small genera of Australia, New Zealand and South Africa would ultimately disappear as a result of the "usurping tendencies of emigrant plants (which had spread naturally to these countries)" and because of "the physique or constitution of the newcomer that enables it to displace other plants". He also attributed the success of plants introduced into Australia by man as partly due to the "abundance of unoccupied ground in Australia" which is still probably a factor in much of the native vegetation in Australia today. Darwin (1859) was also interested in the invasive ability of exotic plants since it fitted well with his theory of natural selection. He attributed the success of exotics to their having reached "a higher stage of perfection or dominating power (as a result of competition and natural selection in the habitat in their native country)". Wallace (1880) added to the ideas expressed above and attributed the success of alien plants in Australia, New Zealand and North America to their "aggressive and colonising" power.

Given that there is adequate dispersal for a species to be a successful coloniser and invader, it must succeed in all of the following stages:

(i) germination

(ii) establishment

(iii) growth to maturity

(iv) reproduction by seed or vegetative means.

The degree of success through which each of these stages or filters is passed provides a measure of the likelihood of a species being an invader. Certain stages may act as a limiting step in success and so differentiate between even closely related plants.

Thus Schinus molle (pepper-tree) is a successful invader in southern California (Nilsen & Muller 1980 a, b). Both S. molle and S. terebinthifolius (broad-leaf pepper-tree) have been grown there for at least a century but only S. molle has become naturalized, even though both taxa are vigorous colonisers. It was shown that S. molle requires less time between seed imbibition and germination which allows root development during the brief periods of ample soil moisture. This demonstrates the limiting nature of, in this case, the first of the above stages. In fact, if S. terebinthifolius was comparable to S. molle in time to germination, both may have become invaders because established plants of S. terebinthifolius have better drought resistance and seedlings have a faster growth rate, with higher root/shoot ratios than S. molle.

The invasive ability of Bromus tectorum (downy brome), a winter annual grass, is apparent in the northern inter-mountain region of the United States where it is displacing the native perennial Agropyron spicatum (wheat grass) (Harris 1967). This is due to the greater success of the annual in passing through each of the above filters — B. tectorum germinates more rapidly at 10°C, has more rapid root elongation in the winter and matures four to six weeks earlier than A. spicatum. This also results in less available soil moisture left for A. spicatum which causes some mortality of this species in the summer.

1.6 Study Plants

It is of value to compare the characteristics of at least potentially invasive species so that predictions may be made about their potential spread and knowledge of the ecology of such species may be used as an aid in their control.

Two principal species were selected for study – C. monilifera (Compositae) and A. longifolia (Mimosaceae). These were chosen because both are at least potentially invasive. This has been adequately demonstrated with A. longifolia in South Africa (Shaughnessy 1980) and probably also with C. monilifera in Australia.

In South Africa, there are two species of the genus Chrysanthemoides, C. incana (Burm. f.) T. Norl. and C. monilifera (L.) T. Norl. Six sub-species of C. monilifera have been described, each with a well defined geographic range in South Africa (Norlindh 1943). Only C. monilifera is known to be present in Australia and only two of its sub-species have been introduced: C. monilifera ssp. rotundata (DC.)T. Norl. (bitou bush) and ssp. monilifera (boneseed) (Gray 1976). Other common names are jungle weed, jungle flower, South African star bush, Higgins Curse and saltbush.

C. monilifera ssp. monilifera has spread rapidly in the last 30 years and is now regarded as a serious threat to considerable areas of native vegetation so that it can be fairly claimed to be invasive (Wheeler 1964; Garnet 1965; Pescott 1968; Welsh 1970; Specht 1972; Anon. 1976; Lane 1981).

There is less evidence concerning the invasiveness of C. monilifera ssp. rotundata although Gray (1976) claims that: "It competes strongly with, and in places totally eliminates, native dune species, e.g. Leucopogon parviflorus (Andr.) Lindl., Correa alba Andr. var. alba, and particularly Acacia longifolia var. sophorae (Labill.) F. Muell., which has a similar growth habit". He offers no experimental evidence, however, for this assertion.

This raises the question: why is C. monilifera so successful and A. longifolia apparently less so if both are invasive species? The very co-existence of these two species was another reason for choosing them for study since the influence of varying habitats and geographical areas can be eliminated. Both were also of interest since various reports cited previously claim they can invade areas of relatively little disturbance where the reasons for success of invasion are less well understood than in very disturbed situations.

Extensive littoral areas in New South Wales contain both C. monilifera ssp. rotundata and A. longifolia var. sophorae and it was for this reason that the bulk of the present study was concentrated on these plants. Where appropriate, however, C. monilifera ssp. monilifera was also considered as well as other species and genera.

FIG. 1.1. Cotyledon (left), first true leaf (right)
and putamina of C. monilifera ssp. rotundata
(left) and ssp. monilifera (right).

1.6.1 Description
1.6.1.1 C. monilifera

The morphological characteristics of the two sub-species of C. monilifera are quite distinct (Table 1.1, Fig. 1.1).

Table 1.1 Morphological differences between C. monilifera ssp. monilifera and ssp. rotundata in Australia.

ssp. monilifera	ssp. rotundata
generally erect shrub, 1-3 m high	sprawling shrub, long decumbent branches, 1-2 m high, 2-6 m wide
leaves toothed, obovate length/breadth ratio 1.9-2.4	leaves entire, broadly obovate length/breadth ratio 1.4-1.6
petiole 0.9-1.1 cm	petiole 2.1-2.4 cm
5-6 bright yellow ray florets	11-13 bright yellow ray florets
putamen globose, length/breadth ratio 1.0-1.1	putamen distinctly obovoid, length/breadth ratio 1.7-1.9

In addition I have observed that the branches of ssp. rotundata which are near the soil surface often act as layers which root at nodes along the stems. Also the cotyledons of seedling plants of ssp. rotundata are obovate whereas those of ssp. monilifera are orbicular.

Data from herbarium specimens indicate that ssp. monilifera flowers between August and October whereas ssp. rotundata flowers over a much longer period, from May to November (Gray 1976).

1.6.1.2 A. longifolia

There are two varieties of A. longifolia (Andr.) Willd. present in Australia: var. longifolia (Sydney golden wattle), a tall shrub and var. sophorae (coastal wattle), a low, bushy, spreading shrub. Most of the present study has been on the latter and, unless otherwise

specified, var. sophorae is referred to where A. longifolia is mentioned. The seedlings of var. sophorae have two to three bipinnate, true leaves; thereafter the plant produces phyllodes which are much more broadly obtuse than var. longifolia. Flowering occurs between August and October. Other botanical details are given by Black (1960). Var. sophorae is recommended for planting as a low windbreak and sand-binder in coastal areas because it has "a fast growth rate" (Whibley 1980) and roots at nodes along its prostrate stems.

1.6.2 History of invasion
1.6.2.1 C. monilifera ssp. rotundata

The history of C. monilifera ssp. rotundata in Australia is not particularly clear but, from herbarium records, it was first known in the Stockton area near Newcastle in N.S.W. in 1908 (Gray 1976), where it was apparently introduced in ballast dumped on the north bank of the Hunter River by South African ships (Cooney, Gibbs & Golinski 1982). No other records of it exist until 1950 when a specimen was collected from the Soil Conservation Service of N.S.W. experimental area at Port Macquarie. Seed was sown extensively by the Soil Conservation Service from 1946 to 1968 for stabilisation of coastal sand drift, after using it in experimental areas at Ballina, Iluka, Mylestom, Port Macquarie and The Entrance North (Mort & Hewitt 1953; Sless 1958 a, b; Zaborowski, pers. comm.). Although ssp. rotundata was the only sub-species used by the Soil Conservation Service, Mort & Hewitt incorrectly describe ssp. monilifera in their report. The only inland planting for sand drift control was near Broken Hill and Menindee where it has subsequently colonised adjacent areas (Cunningham, Mulham, Milthorpe & Leigh 1981).

Mining companies also used this plant for revegetation after beach mining (chiefly for rutile) during this time in the Redhead, Diamond Head, Port Macquarie, Crescent Head, Byron Bay, Hastings Point and Tweed Heads areas (Barr 1965; Zaborowski, pers. comm.).

In the Moruya area on the south coast of N.S.W., it was introduced in 1955 onto Quandolo Island near the mouth of the Moruya River at the request of the local Progress Association who thought that wind-blown sand might block the river! Since then it has spread alarmingly both north and south of this point for at least 10 km either way.

In 1971, the plant was removed from the list of species recommended by the Soil Conservation Service for use in sand drift control and mining companies advised accordingly. Since then, the practice of using it appears to have discontinued. It was once proclaimed a noxious weed in the Newcastle district but subsequently was removed from the list when it began to be used for stabilizing drift areas (Mort & Hewitt 1953).

1.6.2.2 C. monilifera ssp. monilifera

This sub-species was first recorded in Sydney in 1852 from MacLeay's garden; Melbourne in 1858 (and subsequently grown in Melbourne suburbs as a garden plant); Adelaide in 1892 from the West Terrace Cemetery; Armadale, Western Australia in 1948; and Ulverstone, Tasmania in 1931. It was cultivated in most States as a garden shrub and most of the present infestations are escapees from such situations. At one time, plantings to stabilise coastal sand dunes between Nelson and Portland in western Victoria may have been carried out (Garnet 1965).

The Victorian Government was persuaded by the Department of Crown Lands and Survey through its Vermin and Noxious Weeds Destruction Board to proclaim this sub-species a noxious weed in 1969. The arguments used were that "it posed a direct threat to the structure and composition of native bushland and an indirect threat to birds and animals by the alteration of their habitat" (Lane 1976).

1.6.2.3 A. longifolia

A. longifolia was introduced into South Africa as a sand stabiliser in the White Sands area of the Cape Flats near Cape Town in 1827 and 1835 (Shaughnessy 1980). Boucher & Stirton (1978) state that this species has not persisted in these sandy areas and imply that it has invaded areas along rivers in moister localities than where it was originally sown. However, Shaughnessy (1981 and pers. comm.) is of the opinion that this species was planted in both situations and persisted only in moister ones.

At the same time, there appears to be some tolerance for drier areas as it is found to a lesser extent on drier, sandy soils, on clays and in rocky places with sandy soils such as Table Mountain (Boucher & Stirton 1978). These authors state that it has become established in Mountain Fynbos, Lowland Fynbos, Southern Forest, Eastern Cape Forest and Grassland vegetation groups (Acocks 1975).

There has apparently been some difficulty in South Africa in distinguishing between the two varieties of A. longifolia although it is stated that both are present there (Boucher & Stirton 1978). However, only an erect form of A. longifolia has been apparent in photographs from South Africa. If the latter is correct and the prostrate form is not present, several alternative possibilities may have occurred in the past:

1. Both varieties were introduced and only var. longifolia has survived.

2. Only var. longifolia was introduced.

3. Var. sophorae was introduced but has not persisted in the original area of sowing and developed a more upright habit of growth when present in less exposed conditions.

This last explanation is certainly feasible as upright forms of var. sophorae (with similar leaf dimensions and shape to the more prostrate form) are not uncommon in sheltered dune situations in N.S.W.

1.6.3 Distribution
1.6.3.1 C. monilifera ssp. rotundata

This sub-species occurs mainly in coastal areas in Australia from Tathra in southern N.S.W., to Tin Can Bay, Fraser Island and the Wide Bay district in southern Queensland, from latitude $26°0'$ to $36°45'$. It occurs also outside the mainland on Lord Howe Island and in inland areas in N.S.W., near Broken Hill and Menindee (Fig. 1.2).

A survey was conducted in conjunction with the N.S.W. National Parks and Wildlife Service to determine the distribution and abundance of this sub-species on the south coast of N.S.W. between Albion Park (just south of Wollongong) and Ben Boyd National Park near the N.S.W.-Victorian border.

The survey was made by helicopter in early April 1982 which coincided with the onset of flowering. Obviously only adult plants could be noted in this survey but previously (in 1979) occurrences of adults and seedlings had been noted from the ground between Sydney and Tathra.
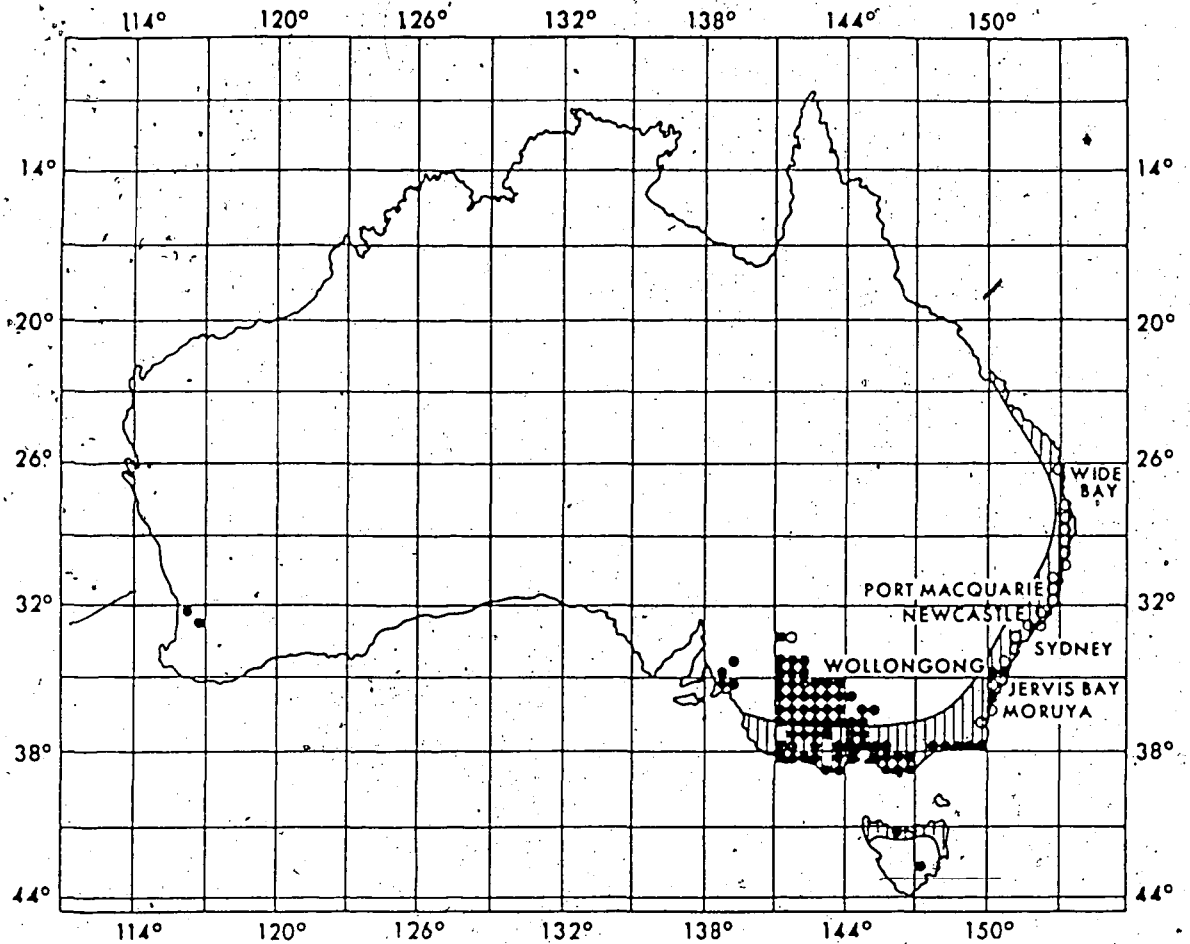
FIG. 1.2. Distribution of <u>C. monilifera</u> ssp. <u>rotundata</u> (o),
ssp. <u>monilifera</u> (•), both sub-species (■) and
generalised distribution of <u>A. longifolia</u> (hatched area)
in Australia.
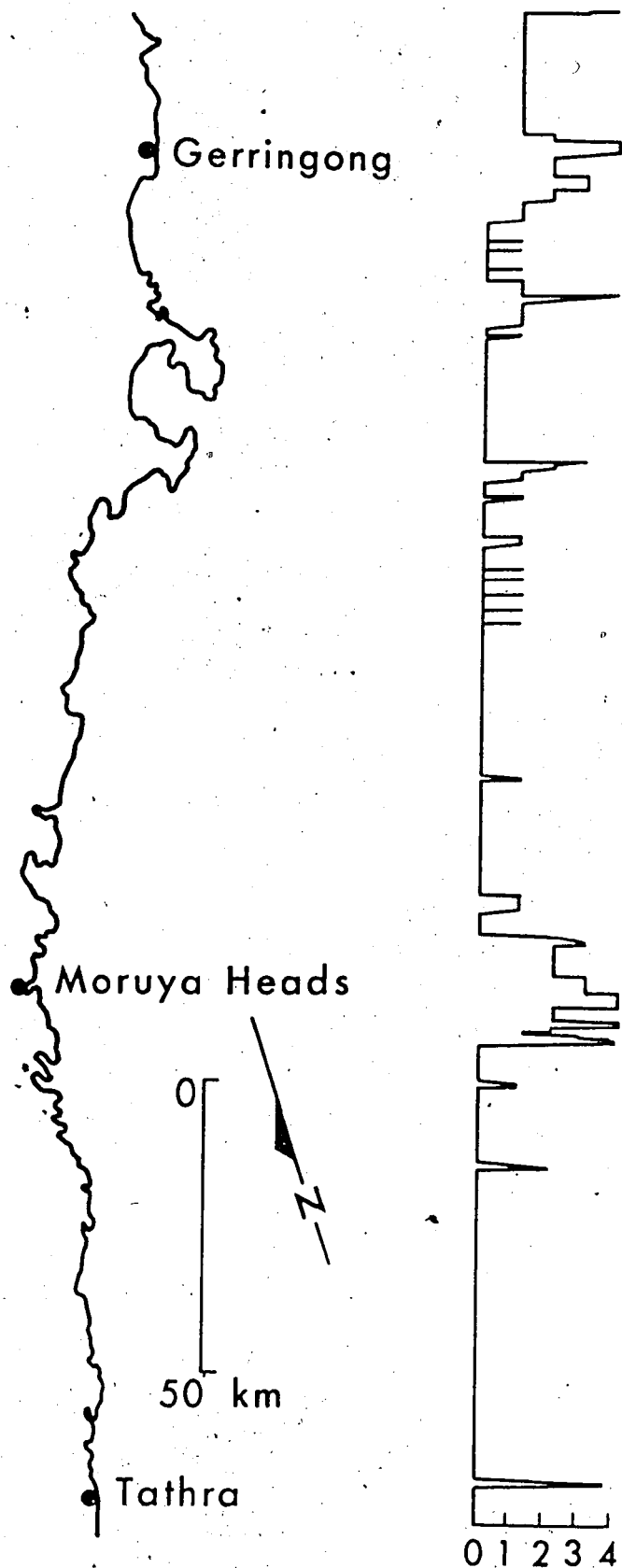
FIG. 1.3. Frequency distribution of C. monilifera ssp. rotundata
from results of an aerial survey on the south coast of
N.S.W. Frequency classes are divided into 0 (absent),
1 (rare, 1-2 plants), 2 (occasional), 3 (common -
frequent but not dominant), 4 (very common - dominant).
Known localities of introduction are shown on the map.
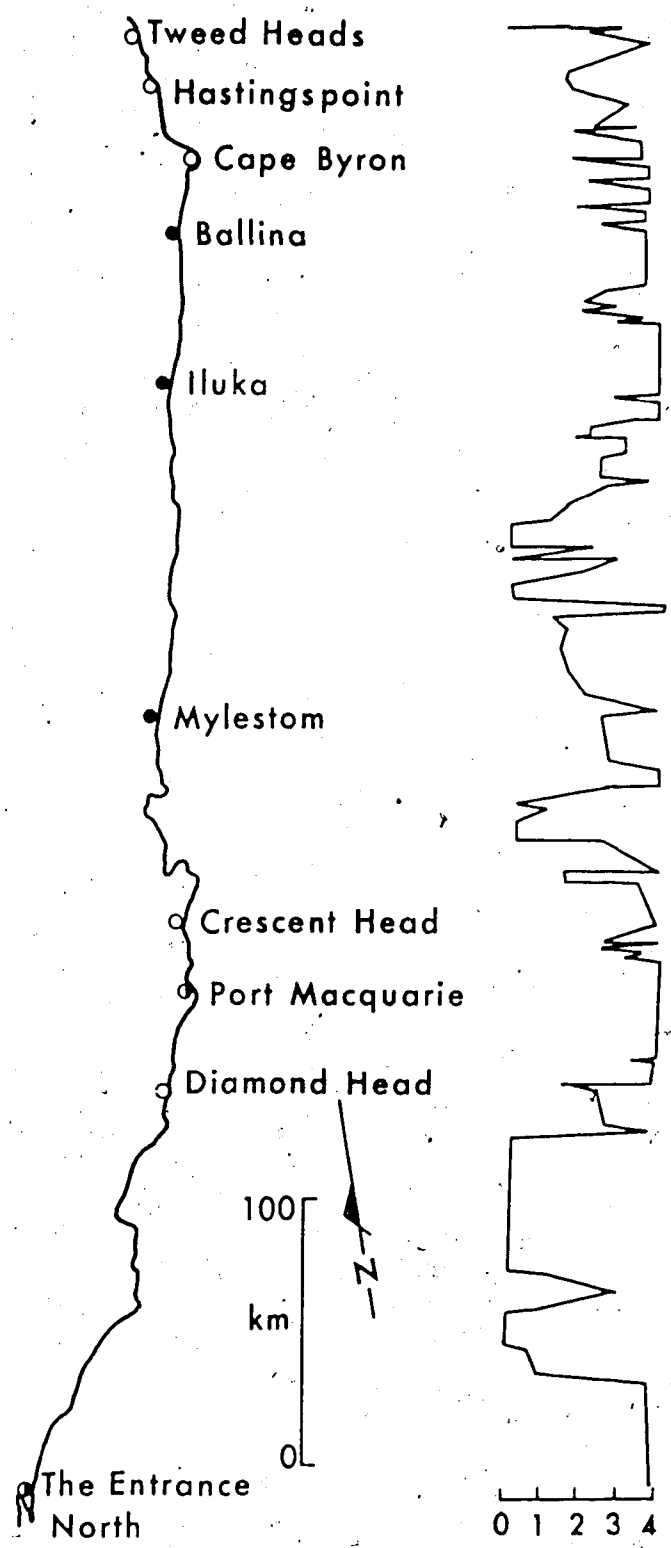
FIG. 1.4. Frequency distribution of C. monilifera ssp. rotundata
from results of an aerial survey on the north coast of
N.S.W. Frequency classes are as in Fig. 1.3. Known
introductions by mining companies (O) and the Soil
Conservation Service of N.S.W. (●) and by both (◐)
are shown.
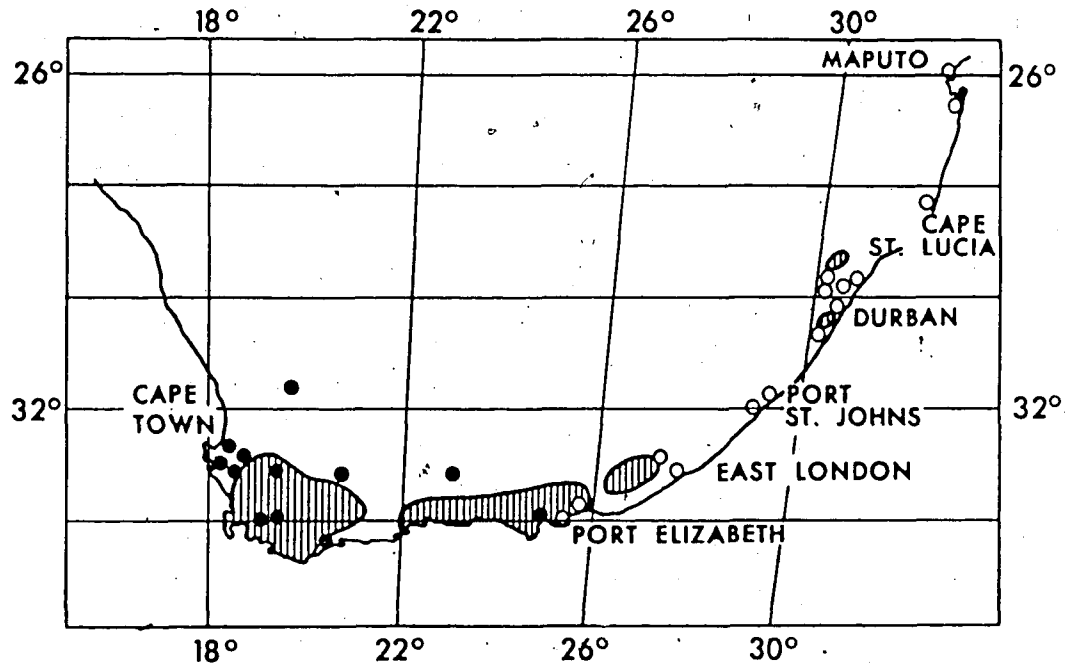
FIG. 1.5. Distribution of C. monilifera ssp. rotundata
(O), ssp. monilifera (●) (from Norlindh 1943) and
A. longifolia (hatched area) (from Milton & Moll 1982)
in South Africa.
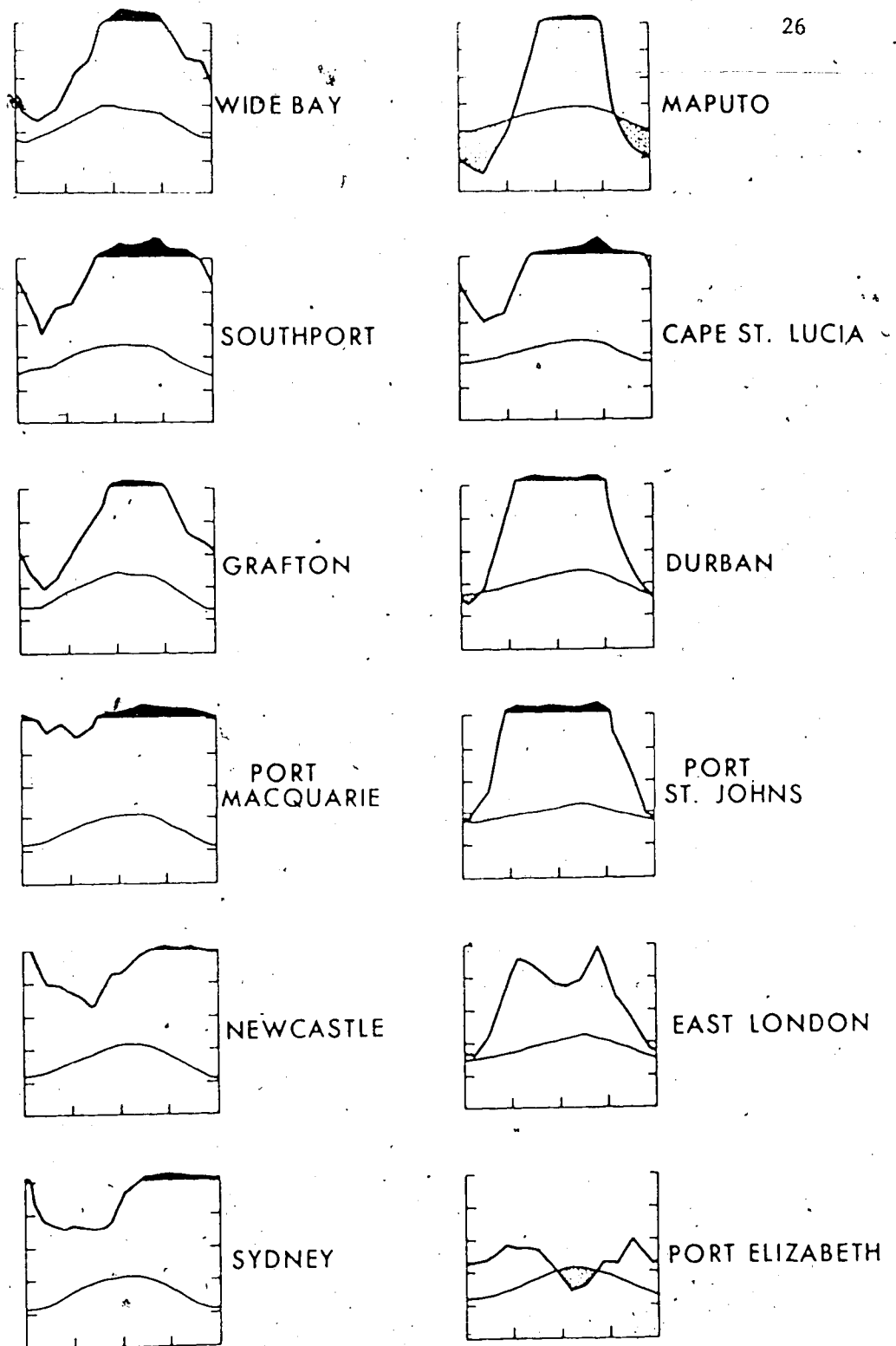
FIG. 1.6. Climate diagrams of localities of occurrence of C. monilifera
ssp. rotundata in Australia (left) and South Africa (right),
matched for similarity in latitude. Approximate latitudes
(from top to bottom) are 26°, 28°, 30°, 32°, 33°, and 34°S.
The thinner bottom curve in each diagram represents monthly
means of temperature (each division is 10°C). The thicker
top curve represents monthly means of rainfall (each division
is 20 mm; rainfall over 100 mm is on a 1:10 scale and shown
in solid black). A period is considered to be arid when the
rainfall curve falls below that of temperature (dotted area)
(from Walter & Lieth 1967).

In the aerial survey, each sampling area (approximately every 0.5 km of coastline) was classified into five categories:

nil (C. monilifera absent)
rare (only 1 or 2 plants)
occasional (scattered plants)
common (plants frequent but not dominant)
very common (the dominant of the vegetation).

Each area was thus able to be given a rating between 0 and 4 which was marked on maps (1:25000 scale), as shown in Fig. 1.3. Approximately 25% of the areas contained some C. monilifera.

A similar survey was done in 1981 on the north coast of N.S.W. from Tweed Heads (near the N.S.W.-Queensland border) to Stockton (just south of Newcastle) (Fig.1.4). The localities on the map indicate areas of introduction of C. monilifera by either the Soil Conservation Service of N.S.W. or by mining companies. These largely parallel the areas of the heaviest concentration of the plant. Approximately 60% of the coastline contained some C. monilifera (A. Love, pers. comm.).

In South Africa, it occurs mainly in the south-eastern coastal area from Port Elizabeth to Maputo, from latitude 26°0' to 34°0' (Norlindh 1943) (Fig. 1.5, 1.6).

1.6.3.2   C. monilifera ssp. monilifera

This sub-species occurs widely in Australia, in mainly coastal and near coastal areas but it is also common in inland areas, particularly in Victoria. It is most widespread in Victoria (Parsons 1973) but occurs also in south-western Western Australia; in the Adelaide Hills and Mt. Lofty Range of South Australia; in Tasmania and near Broken Hill, Sydney and Mollymook in N.S.W., from latitude 32°0' to 42°45' (Gray 1976) (Fig. 1.2).

In South Africa, it occurs mainly in the south-western Cape districts, most collections having been made in the surroundings of Cape Town. However, it is also known from a locality in the Humansdorp district (near Port Elizabeth) in the south-eastern Cape (Norlindh 1943). It occurs from latitude 32°0' to 34°45' (Fig. 1.5).

The only presently known areas in Australia where the two sub-species occur together are at Mollymook on the south coast of N.S.W. and Avalon on the central coast of N.S.W. At Mollymook, ssp. monilifera is mainly on a headland, without any ssp. rotundata.

However, both occur in the same locality at a lower elevation on the
frontal dune system, the closest plants of one sub-species to the
other being approximately 20 metres apart. In this situation,
ssp. monilifera is obviously a garden escapee since several specimens
have been observed in gardens in the area but the origin of
ssp. rotundata in this area is not clear.

At Avalon, I have observed a form intermediate between the two
species, with 8 ray florets and intermediate leaf shape and margins.

1.6.3.3 A. longifolia

In Australia, A. longifolia is chiefly restricted to coastal sand
dunes, in Queensland, New South Wales, Victoria, South Australia and
Tasmania, from latitudes 22°30' to 42°45' (Bentham & von Mueller
1864).

It has been cultivated in Africa, North America and South America
as an ornamental and as a sand binder. It has become naturalised in
Uruguay (Punta del Este), Argentina (Miramar, Bahia Blanca, Villa
Gesell), United States of America (California) and South Africa (Cape
Province, Natal). In South Africa it extends from Hopefield in the
south-western Cape to Grahamstown in the eastern Cape and into Natal,
from latitudes 29°20' to 34°45' (Boucher & Stirton 1978; Milton &
Moll 1982) (Fig. 1.5).

1.7 Plan of Research

From the foregoing, it was apparent that research was needed
firstly to answer the question of whether C. monilifera is invasive in
the sense defined earlier. That is, is C. monilifera expanding from
its originally sown distribution and if so, how is it expanding?
Given that it is not merely filling empty gaps, then the process of
successful invasion implies that it must arise from the invader
displacing occupants (the native species) from their existing niches
(N_1) or from the invader finding a vacant niche (N_2) or a combination
of these ($N_1 + N_2$). The situations N_1 and $N_1 + N_2$ imply that some
reduction in the niche space of some of the occupants will be seen.

In order to test this, the following comparisons need to be made
on the native species between invaded and non-invaded areas:

1. Are the densities less in invaded areas?
2. Are the growth and development rates less

in invaded areas?

3. Are seed and seedling inputs less in
   invaded areas?

4. Are mortality rates of seedlings and established
   plants (before the adult, seeding stage) greater
   in invaded areas?

Some difficulties may arise in comparing plants in non-invaded versus invaded areas especially if the latter are comparatively large. Inherent differences in growth in widely separated areas may confound any differences due to displacement by an invader.

Given that evidence can be found that C. monilifera (C) is displacing native species such as A. longifolia (A), the next logical step is to ascertain the mechanism of displacement, ie how is it occurring? One or more of the following may operate:

1. There is direct adult mortality of A resulting from competition with C.

2. Seed production of A is reduced near C.

3. Seedling emergence and/or establishment of A is reduced near adults of C.

4. Seeds and subsequent seedlings of C arrive at vacant sites before those of A and prevent establishment of A.

5. Seeds of both C and A arrive at vacant sites but subsequent seedlings of C outcompete those of A.

6. The greater numbers of seeds, seedlings and/or adults of C result in a swamping of A.

When these mechanisms of displacement have been investigated, the final question to ask is why C is displacing or is more successful than A. This could be due, for example, to competition at certain times or growth stages for water, nutrients or light, or to C having inherently better physiological properties such as greater water use efficiency. Investigations to attempt to answer the above questions form the basis of the present study.

Chapter 2

Is _Chrysanthemoides_ displacing _Acacia_?

"The alien flora apparently possessed a certain group spirit and cooperative action which permitted it to carry on a mass 'warfare' against the indigenous flora."
(Egler 1942)

"Displacement rarely passes into absolute replacement; after it has reached a certain stage the invaders lose a portion of their vigour, and become less encroaching."
(Kirk 1895).

FIG. 2.1. C. monilifera ssp. rotundata on headland overlooking
the study site at South Beach, Moruya.

2.1 Introduction

It is generally assumed that C. monilifera is having a detrimental effect on native vegetation in Australia. For instance, Gray (1976) stated that, in N.S.W., C. monilifera ssp. rotundata "competes strongly with, and in places totally eliminates, native dune species eg. Leucopogon parviflorus, Correa alba var. alba and particularly Acacia longifolia var. sophorae." Wheeler (1964) and Parsons (1973) reported that, on the western slopes of the You Yangs in Victoria, C. monilifera ssp. monilifera has not only eliminated most of the smaller vegetation but also many trees. In coastal areas of Victoria, this sub-species "dwarfs all weeds by its significance as a danger to bushland" (Anon. 1976)

Certainly the impression one receives in invaded areas is that C. monilifera is outcompeting and eliminating the native vegetation. Further, in some invaded N.S.W. coastal areas, I have seen death of mature plants of species such as A. longifolia, L. parviflorus and Banksia integrifolia, with low numbers of seedlings of these native species. On closer inspection of invaded areas, however, the density of the native species remaining still appears comparatively high while in uninvaded areas, I have also seen death of native species (due apparently to wind, salt or sand blast), with a similar paucity of seedlings. I therefore decided to measure the effect of C. monilifera ssp. rotundata on growth, vigour and development of native vegetation, particularly A. longifolia, in order to ascertain if in fact C. monilifera was displacing such native species.

I decided to select the sand dune complex at Moruya as a study site since it is relatively free from urban development and since it contains C. monilifera ssp. rotundata as well as the three native species mentioned by Gray (1976). Ideally, the growth and development of such native species should be compared in invaded and uninvaded areas. These areas need to be close together to eliminate possible differences in the vegetation due to soil type, climate and recent weather. However, C. monilifera is widespread in the Moruya area (Fig. 2.1) so that I decided to compare a range of densities of C. monilifera within an invaded area. Accordingly, if C. monilifera was displacing the native vegetation, the degree of this displacement might be expected to increase with increasing density of the invasive

species. Despite the above limitations, I also assessed, on a more limited scale, two uninvaded areas south of Moruya.

The Moruya area is part of the Hawkesbury Province (between Port Macquarie and Twofold Bay) in the eastern forest region of Australia (Doing 1981). North of Port Macquarie is the Macpherson Province where C. monilifera also occurs. The climate ranges from temperate to sub-tropical in some of the lowland parts. Rainfall is generally high especially in the northern Province, often between 1000 and 1750 mm per year. The Great Dividing Range separates the coastal area from the Northern and Southern Tablelands of N.S.W. at altitudes from about 600 m in the south to 900 m in the north (Fig. 2.2). Eucalypt and rain forests occur in the region but only dune communities will be considered here.

Austin (1978) described N.S.W. coastal dune communities as having a zonation roughly parallel to the coastline, with "strong circumstantial evidence that it forms part of a succession from beach to sand plain." Austin noted that many of the fore-dunes and active dunes are disturbed, with a resultant mosaic of communities dominated by Spinifex hirsutus, A. longifolia and Carpobrotus glaucescens. The next zone is a thicket community on a stable dune comprised of such species as Monotoca elliptica, Leucopogon parviflorus and Banksia integrifolia. Further back, Eucalyptus botryoides is found growing above B. integrifolia and B. serrata, which gradually merge into a community of such species as E. botryoides and E. pilularis above Macrozamia communis, Pteridium esculentum and Imperata cylindrica.

The study site at South Beach, Moruya is similar to the general coastal complex described above except that some species such as A. longifolia and B. integrifolia occur from the fore-dune to the swale behind the stable dune, with C. monilifera present at an overall density of 0.67 mature plants m^{-2} (Fig. 2.3). Dune heights vary in the area but those shown in Fig. 2.3 are typical.

The soil is a very deep, pale brown, medium, siliceous sand, moderately to strongly alkaline throughout, with little or no profile development with depth.

Monthly averages for precipitation and temperatures in the area are somewhat greater in summer-autumn (Table 2.1) than at other times.
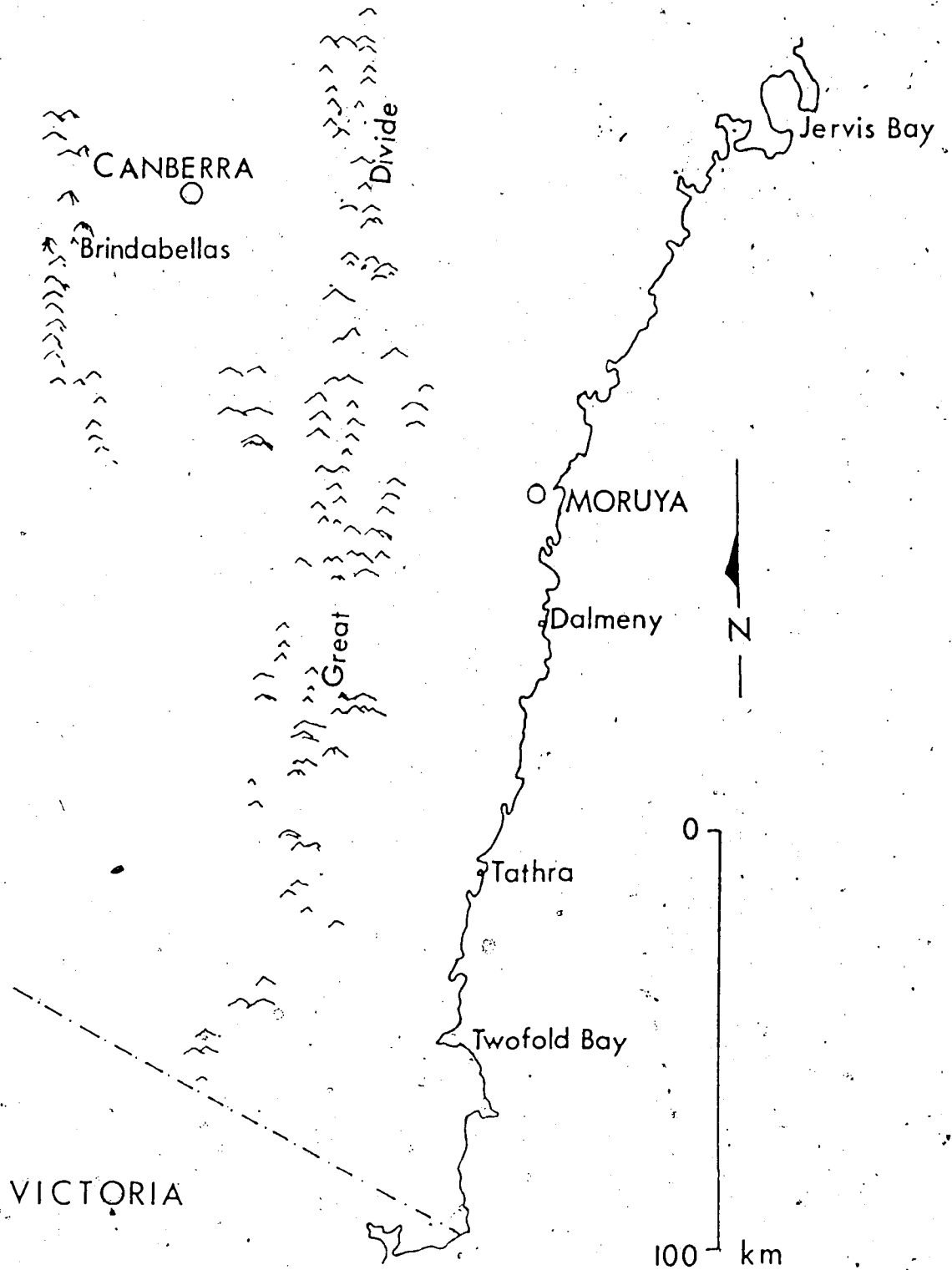
FIG. 2.2. Location of the main study site in coastal N.S.W. near
Moruya in relation to the Great Dividing Range and
Canberra on the Southern Tablelands. An area uninvaded
by C. monilifera was studied at Dalmeny.
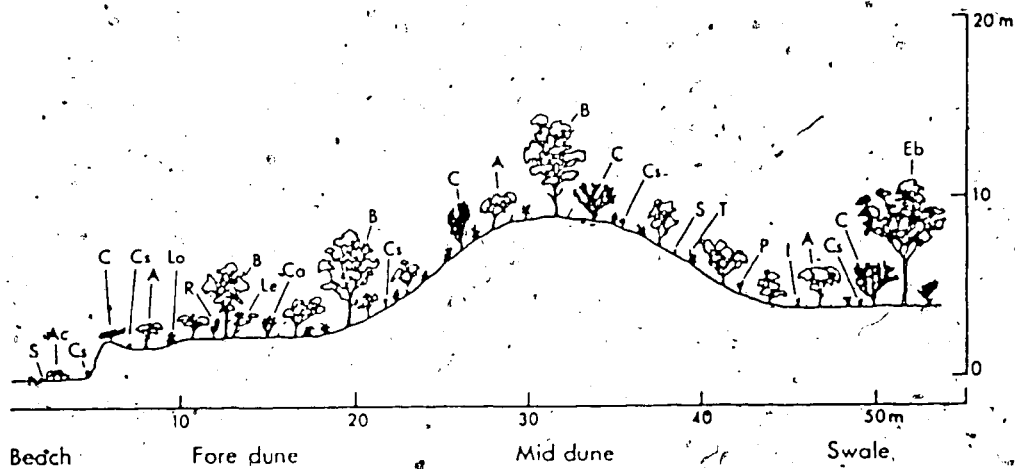
FIG. 2.3. Profile diagram of vegetation on dunes at South Beach, Moruya, showing the most frequently occurring species: A, <u>Acacia longifolia</u>; B, <u>Banksia integrifolia</u>; C, <u>Chrysanthemoides monilifera</u>; Cs, <u>C. monilifera</u> seedlings; Eb, <u>Eucalyptus botryoides</u>; I, <u>Imperata cylindrica</u>; Le, <u>Leucopogon parviflorus</u>; Lo, <u>Lomandra longifolia</u>; P, <u>Pteridium esculentum</u>; R, <u>Rhagodia baccata</u>; S, <u>Spinifex hirsutus</u>; T, <u>Themeda australis</u>; Ac, <u>Atriplex cinerea</u>; Ca, <u>Correa alba</u>.

Table 2.1 Primary climatic data for Moruya*

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual
Rainfall (mm)													Total
Average	97.6	93.7	113.7	85.9	86.5	88.5	55.6	54.4	59.6	78.0	72.6	71.6	953.5
Maximum temperature (°C)													Mean
Average	23.4	23.7	23.0	21.5	18.6	16.5	15.9	16.4	18.0	19.6	21.0	22.1	20.0
Minimum temperature (°C)													Mean
Average	15.7	16.0	14.9	12.0	8.8	6.8	5.7	6.3	8.0	10.6	12.4	14.3	11.0

* Source of data : Moruya Heads pilot station (99 year average)

2.2 Methods

In September 1981, 60 quadrats were selected so that a wide range of densities of <u>C. monilifera</u> was obtained. The number of these quadrats was divided equally between the fore-dune, mid-dune and swale. Each quadrat was 5 x 5 m and 16 sub-quadrats, each 0.3 x 0.3 m, were marked out within each of these in a 1 m grid pattern.

In each quadrat an outline map of the projected ground cover of each species was made and the following were recorded:

(a) species

(b) height of each species

(c) stage of each species (vegetative, bud, flowering, seeding)

(d) percentage cover of each species

(e) percentage cover of litter and bare ground

(f) occurrence of any dead species or dead branches

(g) number of seedlings of each species.

In each quadrat, the following were calculated for each species:

(i) frequency of occurrence

(ii) mean height

(iii) maximum height

(iv) most advanced growth stage

(v) cover

(vi) volume (% cover x mean height).

The figure for cover which was used in analyses was that obtained by tracing the outline of each species in the outline map on a digitiser. This was considered preferable to the data in the sub-quadrats since a larger quadrat area was covered which was more representative of each species.

Prior to analysis, values for cover and frequency were arcsine transformed. Analyses were carried out both on an overall basis (n=60) and on each dune position (n=20).

Similar quadrats were assessed for points (a), (d), (f), (g) above in uninvaded areas at Dalmeny and Congo (30 and 2.5 km south of Moruya respectively) (12 quadrats in each locality, divided equally

between fore-dune, mid-dune and swale).

2.3 Results
2.3.1 Invaded area

C. monilifera was the most frequent species and had the highest ground cover, followed by A. longifolia and Lomandra longifolia (Table 2.2). The frequency and ground cover of C. monilifera were negatively correlated with similar parameters of some other species, particularly A. longifolia (Table 2.3). This may be a reflection of the similarity in growth form between C. monilifera and A. longifolia or the frequent occurrence of A. longifolia in the quadrats. Although such correlations of C. monilifera with most species were not significant, 66 out of 84 correlations were negative (Table 2.3).

Similarly, the mean height) of C. monilifera was negatively correlated with the frequency, volume and cover of A. longifolia (Pearson's correlation coefficients of -0.53, -0.38, -0.38 respectively, $P \leq 0.01$). The mean heights of C. monilifera and A. longifolia were greatest on the mid-dune and swale respectively (ANOVA, $P \leq 0.05$).

The above correlations were determined on an overall basis (not taking dune positions into account). It is thus possible that since some species prefer different dune positions (Table 2.2), this may have influenced the results. For example, the frequency of C. monilifera was significantly higher on the mid-dune than the swale but the opposite was true of A. longifolia (ANOVA, $P \leq 0.05$) (Table 2.2). If only plants at the seeding stage were included in the analysis, similar results were obtained (Table 2.4); no seeding A. longifolia were recorded on the fore-dune.

Table 2.2 Percentage frequency and ground cover of species in three dune positions
(n=20 in each) in an invaded area in September 1981

Species	Frequency			Ground cover		
	Fore	Mid	Swale	Fore	Mid	Swale
Chrysanthemoides monilifera	64.1 ab	78.4 a	57.2 b	37.5 a	43.3 a	31.9 a
Acacia longifolia	28.8 ab	22.5 b	38.1 a	14.9 a	12.8 a	20.6 a
Lomandra longifolia	31.3 a	20.6 a	30.0 a	7.8 a	7.1 a	11.7 a
Leucopogon parviflorus	24.1 a	16.6 ab	8.8 b	12.7 a	7.2 ab	2.4 b
Spinifex hirsutus	31.6 a	14.4 b	10.9 b	0.7 a	0.1 a	0.1 a
Pteridium esculentum	0.6 a	5.6 a	31.9 b	0.03 a	0.3 a	2.1 b
Correa alba	7.5 a	1.3 a	0	2.9 a	0.5 a	0
Olearia axillaris	1.6 a	0.6 a	1.3 a	0.2 a	0.2 a	0.1 a
Imperata cylindrica	0.3 a	0	40.6 b	0.01 a	0	0.2 b
Banksia integrifolia	10.0 a	5.0 a	4.7 a	5.2 a	3.8 ab	1.3 b
Carpobrotus glaucescens	3.4 a	1.6 a	0	0.9 a	0.1 a	0
Pelargonium australe	1.9	0	0	0.01	0	0
Rhagodia baccata	6.6 a	0.3 a	0	2.6 a	0.3 a	0
Oxalis corniculata	2.5 a	1.9 a	0	0.01 a	0.01 a	0
Themeda australis	0	0	10.0	0	0	0.1
Eragrostis sp.	0	0	1.3	0	0	0.02
Stipa sp.	0	0	12.8	0	0	0.07
Malva sp.	0	0	4.7	0	0	0.02
Eucalyptus botryoides	0	0	3.4	0	0	3.1
Juncus sp.	0	0.9	0	0	0.01	0
Trifolium sp.	0	0	0.6	0	0	0.01
Helichrysum obcordatum	0	0	0.9	0	0	0.02

Values within each parameter of each species followed by the same letter are not
significantly different at $P = 0.05$ (Bartlett's test). No ANOVA was done where
species occurred in only one position.

Table 2.3 Pearson's correlation coefficients of frequency and cover of
C. monilifera with frequency and cover of other species with
all dune positions combined (n=60)

Species	Frequency of C. monilifera		Cover of C. monilifera	
	Frequency	Cover	Frequency	Cover
A. longifolia	-0.39**	-0.50**	-0.39**	-0.45**
L. longifolia	-0.20	-0.43**	-0.23	-0.51**
L. parviflorus	0.05	0.04	-0.15	-0.20
S. hirsutus	-0.20	-0.19	-0.06	-0.10
P. esculentum	-0.04	0.06	0.02	0.01
C. alba	-0.08	-0.04	-0.05	-0.10
O. axillaris	-0.03	-0.02	-0.02	-0.04
I. cylindrica	-0.19	-0.22	-0.08	-0.13
B. integrifolia	0.06	0.12	0.01	0.03
C. glaucescens	-0.18	-0.12	-0.02	-0.03
P. australe	-0.16	-0.19	-0.12	-0.16
R. baccata	-0.10	-0.14	-0.10	-0.12
O. corniculata	-0.19	-0.30*	-0.15	-0.21
T. australis	-0.22	-0.28*	-0.21	-0.30*
Eragrostis sp.	-0.04	-0.15	-0.11	-0.18
Stipa sp.	-0.10	-0.08	-0.03	-0.04
Malva sp.	-0.06	-0.04	-0.02	-0.05
E. botryoides	0.07	0.21	0.13	0.24
Juncus sp.	0.02	0.04	-0.09	-0.13
Trifolium sp.	-0.05	-0.06	-0.05	-0.07
H. obcordatum	-0.03	0.06	0.05	0.16

* $P \leq 0.05$ ** $P \leq 0.01$

Table 2.4 Percentage frequency of C. monilifera and
A.longifolia at the seeding stage in three dune
positions (n=20 in each) in September 1981

Species	Fore-dune	Mid-dune	Swale
C. monilifera	48.5 a	60.0 a	35.6 b
A. longifolia	0	2.7 a	6.0 b

Values in each row followed by the same letter are not
significantly different at P = 0.05 (Bartlett's test).

Accordingly, I repeated the correlations of frequency and ground
cover of C. monilifera with those of the other species at each of the
three dune positions (Table 2.5). Again, A. longifolia was the
species most affected, with most negative correlations on the
fore-dune, followed by the swale. However, two of the quadrats on the
mid-dune had a large proportion of dead stems of C. monilifera. If
these quadrats were treated as missing data in the analysis, the
negative correlation with cover of A. longifolia on the mid-dune also
became significant.

Cover of C. monilifera was negatively correlated with maximum
height of A. longifolia on the fore-dune (a coefficient of -0.48,
$P \leq 0.05$). The parameter of volume (cover x mean height) was
calculated to give an estimate of biomass but gave similar
correlations to cover only.

Although C. monilifera had an effect on some species besides
A. longifolia, it is possible that this may have been an additive
effect due to the two dominant species. In order to test this, the
values for cover of C. monilifera and A. longifolia were summed.
There was then a negative correlation with the cover of Lomandra (a
coefficient of -0.54, $P \leq 0.01$). Multiple regressions were then
carried out, using three independent variables: 1. cover of
C. monilifera; 2. cover of A. longifolia; 3. dune position. The
relative effect of these variables on cover of some minor species
could then be determined. Results of these regressions confirmed that
both presence of C. monilifera and A. longifolia affected cover of
Lomandra, position being relatively unimportant (Table 2.6). However,

Table 2.5 Pearson's correlation coefficients of frequency and cover of
C. monilifera with frequency and cover of other species in three dune
positions (n=20 in each). Only species with at least one significant
value are listed

Species	Parameter	Frequency of C. monilifera			Cover of C. monilifera		
		Fore	Mid	Swale	Fore	Mid	Swale
A. longifolia	Freq.	-0.60**	-0.25	-0.24	-0.81**	-0.10	-0.32
	Cover	-0.59**	-0.21	-0.59**	-0.72**	-0.05	-0.57**
L. longifolia	Freq.	-0.18	-0.20	-0.35	-0.30	-0.34	-0.29
	Cover	-0.29	-0.30	-0.55**	-0.46*	-0.51*	-0.47*
L. parviflorus	Freq.	-0.03	-0.12	-0.05	-0.12	-0.37	-0.05
	Cover	-0.02	-0.05	-0.01	-0.08	-0.51*	-0.11
O. corniculata	Freq.	-0.37	-0.40	–	-0.25	-0.35	–
	Cover	-0.42	-0.59**	–	-0.30	-0.36	–
T. australis	Freq.	–	–	-0.21	–	–	-0.33
	Cover	–	–	-0.32	–	–	-0.45*

* P ≤ 0.05   ** P ≤ 0.01

Table 2.6 Multiple regressions of cover of C. monilifera (C*) and A. longifolia (A*) and dune position with cover of eight other species (R values are in parentheses)

Species	Constant	B coefficient				
		C*	A*	Fore-dune	Mid-dune	Swale
L.longifolia	33.0	-0.4(0.5)	-0.3(0.6)	–	–	4.3(0.6)
L.parviflorus	11.4	-0.2(0.4)	–	12.1(0.4)	6.3(0.5)	–
S.hirsutus	1.0	–	–	2.1(0.4)	–	–
P.esculentum	2.6	–	-0.1(0.6)	–	1.4(0.6)	2.6(0.5)
C.alba	0.5	–	–	3.4(0.3)	–	–
I.cylindrica	0.03	–	–	–	–	2.7(0.9)
B.integrifolia	16.6	-0.1(0.4)	-0.2(0.3)	–	–	-3.8(0.4)
C.glaucescens	0.3	–	–	2.1(0.3)	–	–

FIG. 2.4. Seedlings of C. monilifera ssp. rotundata under
parent plant on the mid dune. Note single seedling
of A. longifolia (arrowed).
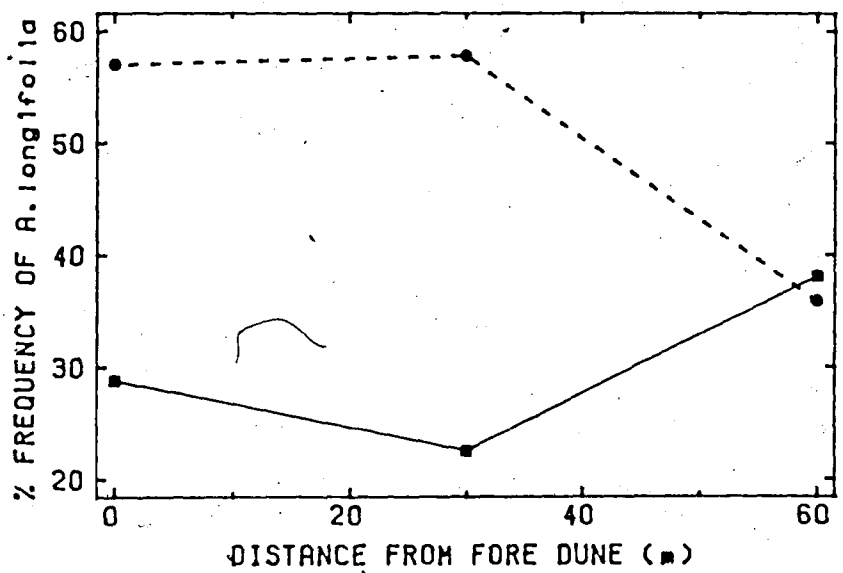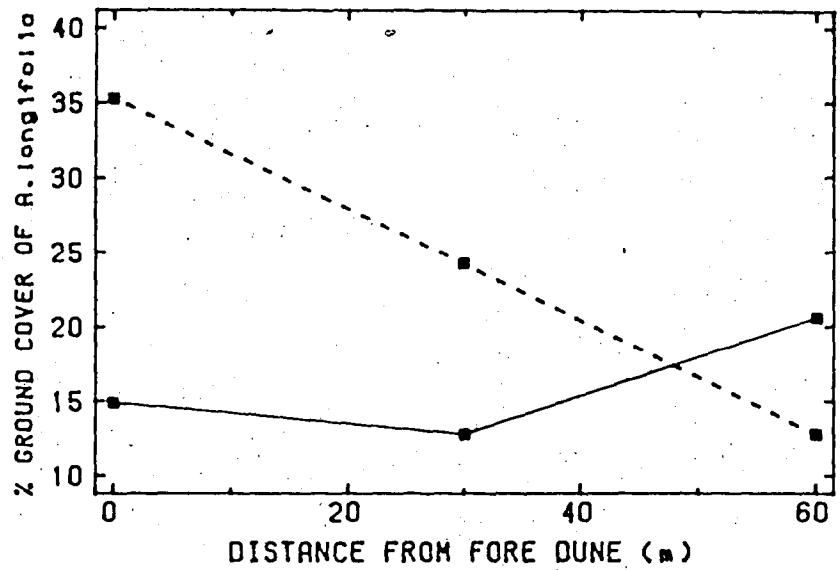
FIG. 2.5. Ground cover (top) and frequency (bottom) of
A. longifolia in areas uninvaded (dotted lines)
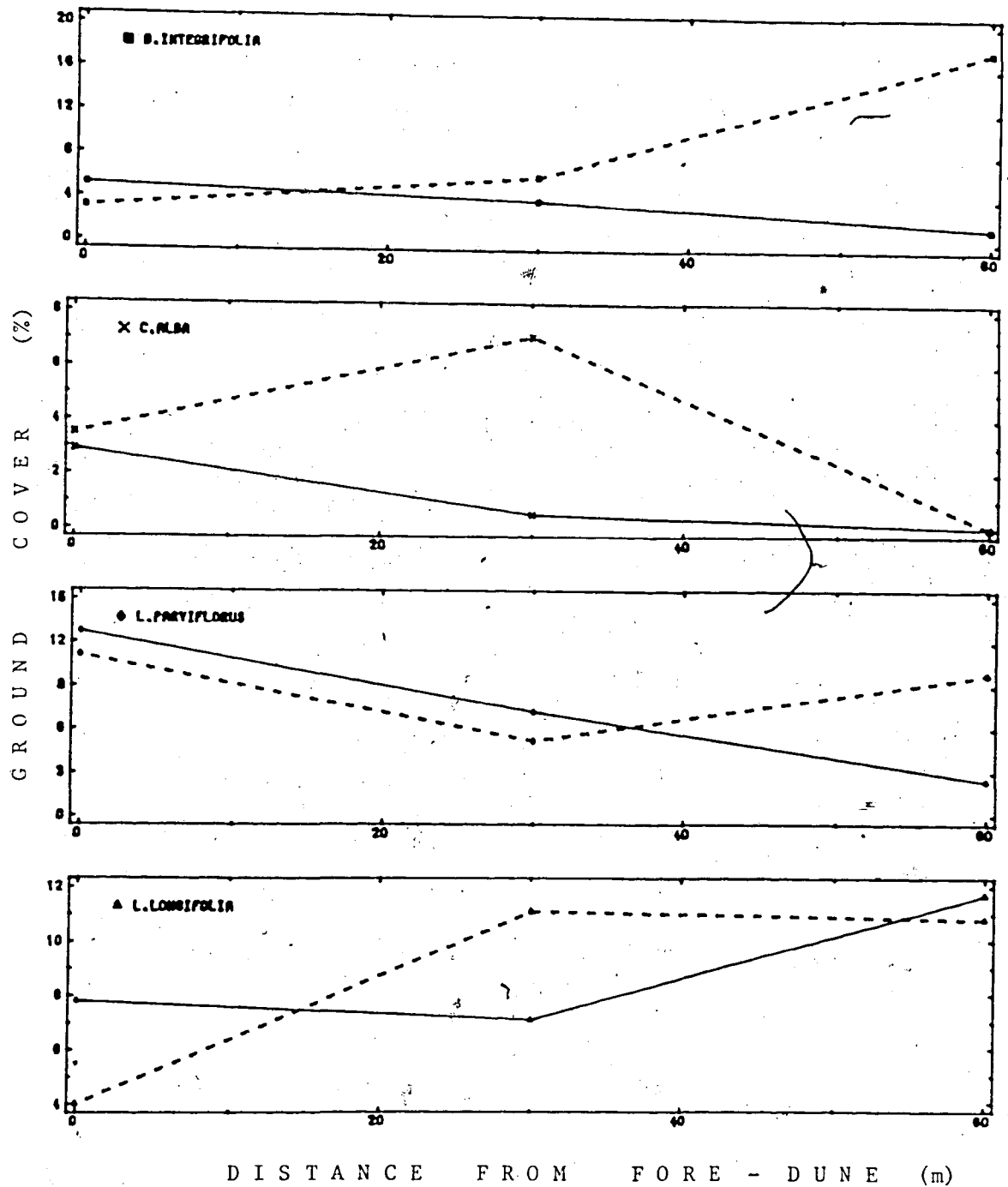and invaded (solid lines) by C. monilifera.

FIG. 2.6. Percentage ground cover of (from top to bottom)
Banksia integrifolia, Correa alba, Leucopogon parviflorus
and Lomandra longifolia in areas uninvaded (dotted lines)
and invaded (solid lines) by C. monilifera.

L. parviflorus, S. hirsutus, C. alba, I. cylindrica and C. glaucescens were affected more by position than by presence of potential competitors. A. longifolia was more important than C. monilifera in affecting cover of P. esculentum and B. integrifolia.

There were very few seedlings of any native species present. Those of A. longifolia occurred sporadically under mature plants of both A. longifolia and C. monilifera at densities of < 0.1 m^{-2} (Fig. 2.4). B. integrifolia was the only other native species recorded in the seedling stage but only one plant occurred in the quadrats. On the other hand, densities of seedlings of C. monilifera were high (Fig. 2.4), means for the fore-dune, mid-dune and swale being 31, 114 and 13 m^{-2} respectively.

2.3.2 Uninvaded areas

Similar species were recorded in the uninvaded areas to those in the area invaded by C. monilifera except that two other introduced species (Rubus fruticosus L. agg. and Conyza sp.) were also present as minor species. A. longifolia was again the most frequent native species but, unlike the invaded area, frequency and ground cover of this species was greater on the fore- and mid-dune than the swale (Fig. 2.5) and plants at the seeding stage were present in all positions. Frequency and ground cover of A. longifolia in the swale were similar in both invaded and uninvaded areas. Ground covers of other species were also comparatively similar between uninvaded and invaded areas, especially on the fore- and mid-dune (Fig. 2.6).

Seedlings of native species were again rare; A. longifolia was the only species recorded and was found only on the fore- and mid-dune at densities of < 0.1 m^{-2}.

2.4 Discussion and summary

It appears that C. monilifera is not merely filling empty gaps in the vegetation, but is actively displacing at least A. longifolia from it's existing niche in the ecosystem. This conclusion is supported by the inverse correlations found between frequency and ground cover of C. monilifera and frequency and ground cover of A. longifolia (Table 2.2). Although there is the possibility of habitat or dune position preference by A. longifolia, as well as the effect of C. monilifera, on growth and development of A. longifolia, the influence of

C. monilifera appears the more feasible in view of the results obtained from uninvaded areas. These show a decrease in cover and frequency of A. longifolia from fore-dune to swale (Fig. 2.5) and agree with the general concept of A. longifolia being predominantly a fore-dune species (Austin 1978). This is in contrast to the distribution of A. longifolia in the invaded area (Table 2.2) and the absence of plants at the seeding stage on the invaded fore-dune (Table 2.4).

Although there was some evidence that C. monilifera limits the growth of species other than A. longifolia such as Lomandra (Tables 2.3, 2.5), there was little difference in ground cover of Lomandra between invaded and uninvaded areas (Fig. 2.6). This may have been due to a greater effect by more A. longifolia in the uninvaded area than that shown in the invaded area (Table 2.6).

Nevertheless, there appears little doubt that C. monilifera is posing a serious threat to the integrity of the native vegetation even if only the dominant species is being replaced. Several other observations confirm this conclusion, but these will be described in later chapters (eg. the effect of C. monilifera on growth and seed production of A. longifolia in Chapter 7). This situation may also deteriorate further since populations of C. monilifera have been building up in the study area only in the last 25 years (Chapter 1) and since Acacia species are relatively short-lived in Australia (Costermans 1981). At one end of the scale, the maximum life span of A. pulchella, a coastal species of Western Australia, was estimated at close to only 13 years (Monk, Pate & Loneragan 1981). In uninvaded areas it would be expected that Acacia populations would be replenished by seedlings. However, in invaded areas, Acacia seedlings would encounter interspecific competition not only with larger numbers of C. monilifera seedlings but also with mature plants. It follows that a difference in seedling numbers should be expected between invaded and uninvaded areas. However, the numbers found in both areas were too low for statistical treatment and so I examined the mechanism of displacement of A. longifolia by C. monilifera, especially in the seedling stage, in more detail. The following chapters report the results of these investigations.

Chapter 3

Seed pools of Chrysanthemoides and Acacia

"Blackberries and boneseed compete with the native pioneers (such as
wattles and dogwood) and prevent the natural succession which
normally occurs after disturbances. Their ability to re-establish
from seed makes them the most significant weeds of Victoria's
bushland. Eradication of all dormant seeds in the soil would be
necessary before an area could be regarded as safe from
reinfestation."
(Anon. 1976)

"... and then the road ran for miles between Australian wattles.
These show a flash of golden flowers for two or three weeks in the
spring, but for the rest of the year they are dull and scraggy, and
all the while they are spreading over the Cape Flats and destroying
the native heaths and proteas, which cannot stand up against their
vulgar, pushing ways."
(Fairbridge 1924)

Introduction

Success as a plant invader may be associated with a   high   level
of   seed output and a large soil pool of long-lived seeds, subject to
low levels of predation.   These are some of   the   characteristics   of
the   "ideal   weed"   (Baker   1974).   Plant invaders may not "achieve"
Baker's ideal, however, because there is often a "trade-off"   between
seed number and seed size (Harper 1977).

In addition, in their native areas, potential invaders   may   not
reach that   potential   because   of the likelihood of a high level of
predation, thereby limiting the numbers of   seeds   produced   and   the
size   of   the   soil   seed   pool, as well as reducing the half-life of
seeds   in   that   pool.   Thus   species such as   C. monilifera   and
A. longifolia   may   be   able   to   realise   their potential invasiveness
only when they can "lose" their   predators   in   areas   outside   their
native   country,   as   demonstrated   for   A. longifolia in South Africa
(Boucher & Stirton 1978, Milton & Hall 1981).

As outlined in Chapter 1, I decided to examine firstly the   seed
stage   in   the   life   cycle   of   C. monilifera   and   A. longifolia to
determine its relative importance in   invasiveness.   The   components
investigated were:

1.   Flowering and seed production;
2.   Seed predation and dispersal;
3.   Soil seed pool; and
4.   Seed longevity.

High levels in all of these components except predation   should   give
an   initial   advantage   to   a plant invader although the seedling and
more mature stages, which will be considered in later   chapters,   are
also important in success.

Data were   collected   on   C. monilifera   ssp. rotundata   and
A. longifolia   var. sophorae   at   Moruya   between   1980   and 1982 for
components 1, 2 and 3 above and between 1979 and 1982   for   component
4.   C. monilifera ssp. monilifera and Banksia integrifolia were also
included for comparison of seed longevity.

3.1 Flowering and seed production
3.1.1 Introduction

Many species considered as weeds have a high potential for prolific flowering and seed production (as reviewed by Kolk 1979). For C. monilifera and A. longifolia the only reports of seed production in areas outside their native country are by Lane (1976), working with C. monilifera ssp. monilifera in Victoria, who reported a yearly seed set of 50,000 seeds per plant, while for A. longifolia in South Africa, Milton & Hall (1981) recovered 5,200 viable seeds m^{-2} of trap under mature plants. In this study, seed production of C. monilifera ssp. rotundata and A. longifolia was measured over a period of 2 years and flowering over 1 year.

3.1.2 Methods

In similar dune positions at Moruya to those in Chapter 2, all inflorescences on five plants of C. monilifera, varying from 2 to 5 m in diameter, were tagged as they appeared in 1980. Of these inflorescences, 160 were selected and between January 1980 and March 1980, the numbers of ray florets and of seeds subsequently developing were counted on each.

With A. longifolia, the number of inflorescence spikes was counted on a selected terminal branch of each of 40 randomly selected plants in August and September 1980. The proportion of total spikes on the plant represented by the branches counted was estimated and the number of spikes per plant calculated. The number of flowers on each of 100 spikes selected at random was recorded also. On the same branches, the numbers of mature pods formed were counted in November 1980.

A further 600 pods were selected at random and the seeds were counted in each pod; seed abortion was estimated by the number of shrivelled seeds. The viability of the apparently whole seeds was determined by cutting open the seeds and testing with 2, 3, 6 -triphenyl tetrazolium chloride (Isely 1952). In November 1981 pods and seed viability were again assessed on 40 plants, on branches of similar diameter (10 mm).

Seed fall of C. monilifera was measured between May 1980 and February 1982 by placing circular seed traps (30 cm diameter metal frames covered with fibreglass mesh) above-ground and 1 m in from the edge under 20 plants. With 10 of the plants, an additional trap with

bird wire over the mesh was used to check on seed predation after seed fall. With five of the plants, a further trap was placed at the centre of the plant to check on variability.

At the end of each month, seeds and litter were recovered from each trap, dried and weighed. The seeds were counted and classified as either whole (viability was then tested with tetrazolium. chloride), sterile (shrivelled or unfilled) or open (usually only the pericarp present which was split in two or three).

With A. longifolia similar seed traps were placed 1 m in from the edge under 20 plants and at the centre of five of these plants in September 1980. Seeds and pods were collected weekly (to minimise predation) in December 1980, January and December 1981 and January 1982 since seed fall occurred only in these months. Seed viability was tested in December and January each year.

3.1.3 Results
3.1.3.1 C. monilifera

Although some flowers were present every month, there was a pronounced peak in late autumn (Fig. 3.1). There was an annual production of 3130 ± 530 inflorescences per plant. The number of ray florets ranged from 11 to 13 per inflorescence (Fig. 3.2a), with inflorescences producing from 0 to 13 green fruits 2 weeks later (Figs. 3.2b, 3.3). These turned black after another 2 weeks and the fruits lost most of their fleshiness and fell to the ground a further 2 weeks later (6 weeks from flowering), so that most seed fall occurred in winter (in June) each year (Fig. 3.4). Seed production from January to April 1980 was estimated in the 1980 total in Table 3.1. Mean plant size was 3.1 m^2; there was an annual production of 20670 ± 2420 whole seeds per plant. Viable seeds per plant in Table 3.1 were estimated from trap figures and do not include seeds removed from plants (see section 3.2).

3.1.3.2 A. longifolia

All of the plants examined flowered between August and October (Fig. 3.1). Since spikes measured in 1980 represented 9.6% of the total, there were over 1500 spikes per plant but only 100 seeds per plant. (Table 3.2). The year 1980 was the driest in the past century (471 mm compared with an average of 954 mm). In 1981, rainfall was 990 mm and seed production much higher (Table 3.2).

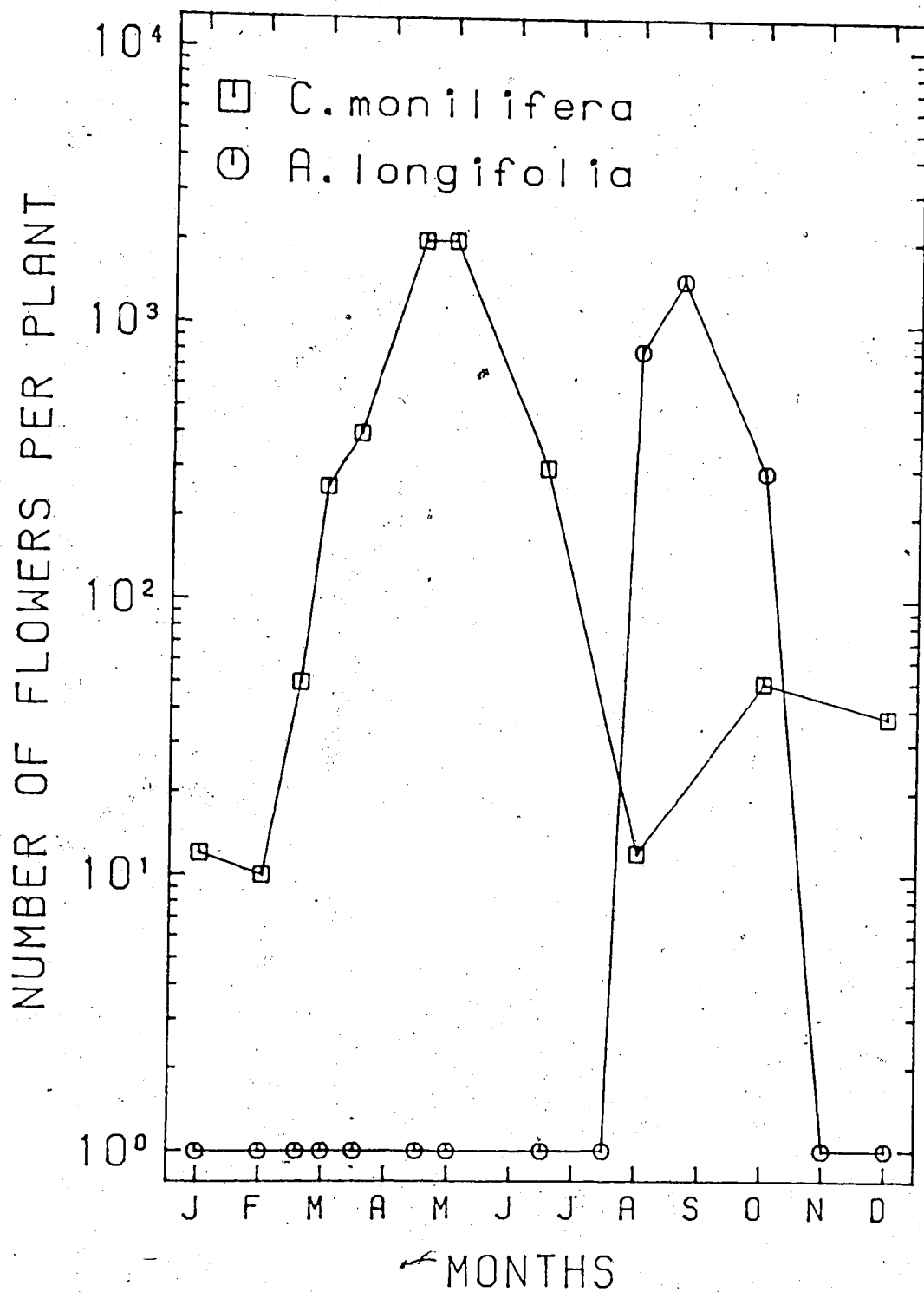FIG. 3.1. Number of flowers per plant of C. monilifera (□) and
of inflorescences per plant of A. longifolia (0)
over a period of 12 months.
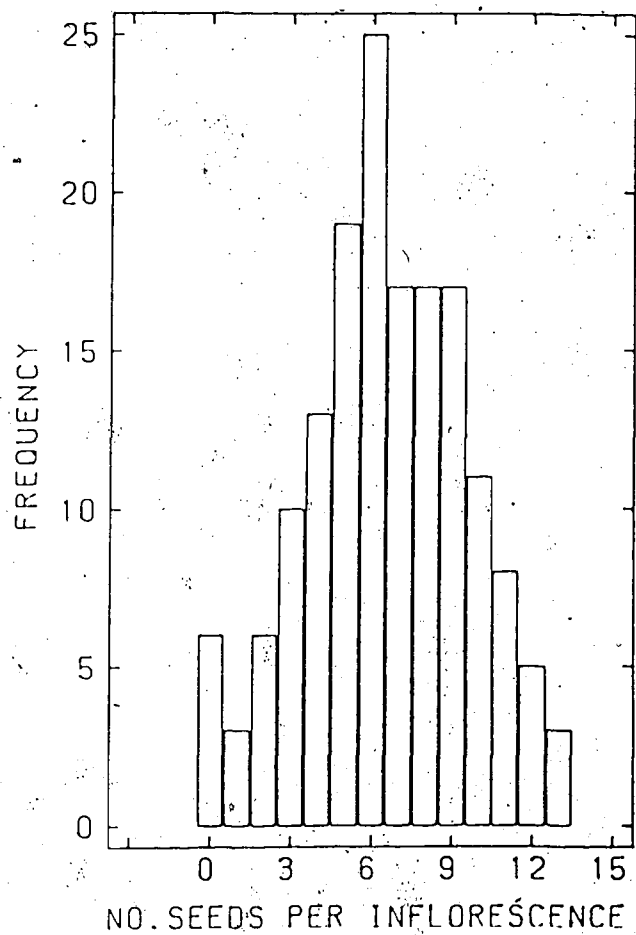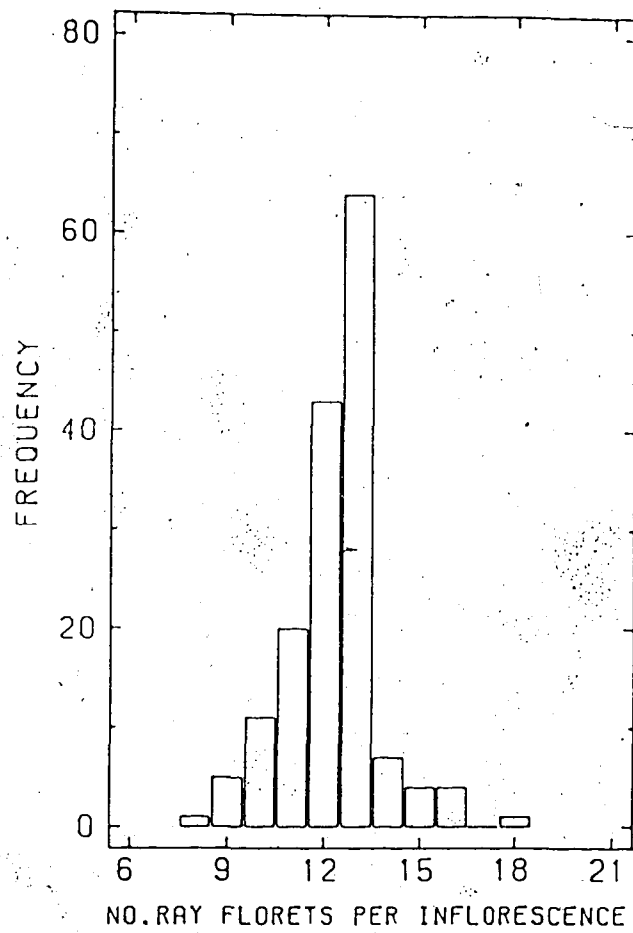
FIG. 3.2. Frequency distribution, expressed as the number of observations (n=160) of (a) the number of ray florets per inflorescence and (b) the number of seeds per inflorescence of C. monilifera ssp. rotundata.

FIG. 3.3. Inflorescences and fruits of C. monilifera ssp. rotundata.
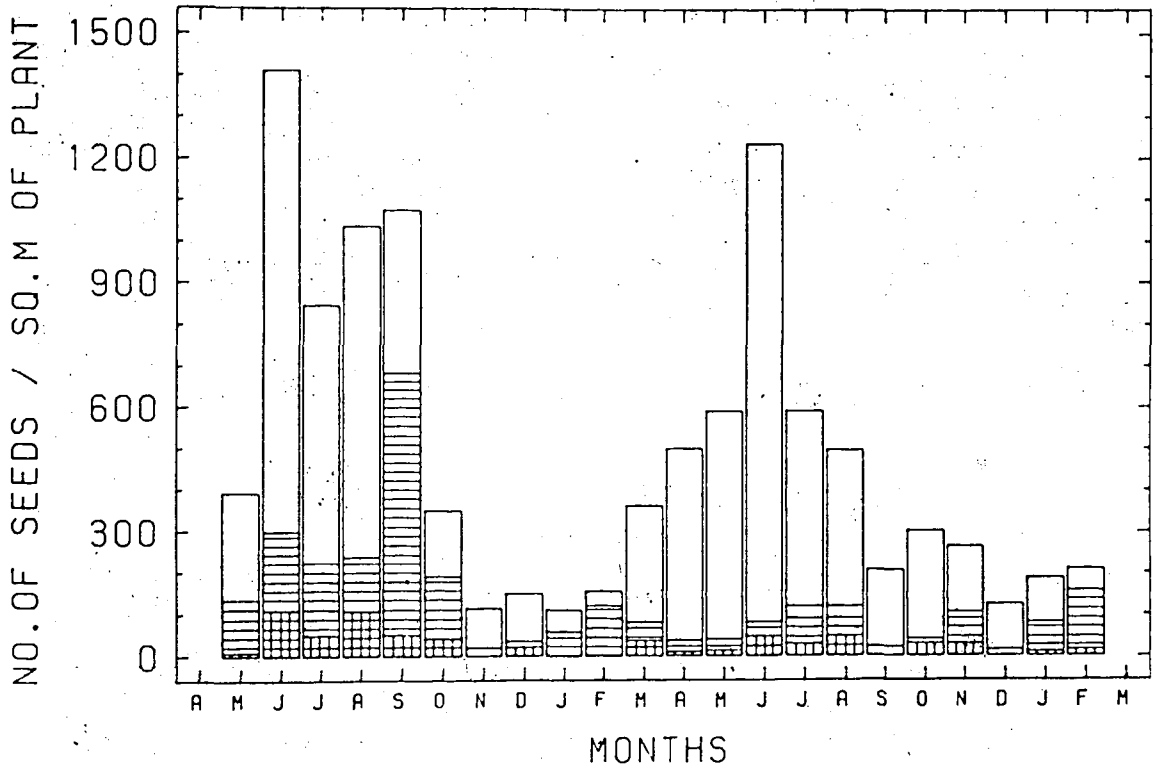
FIG. 3.4. Seed production of C. monilifera between May 1980 and February 1982, expressed as the number of seeds m^{-2} of plant, from seeds collected in traps and classified as whole (□), open (⊟) or sterile (⊞).
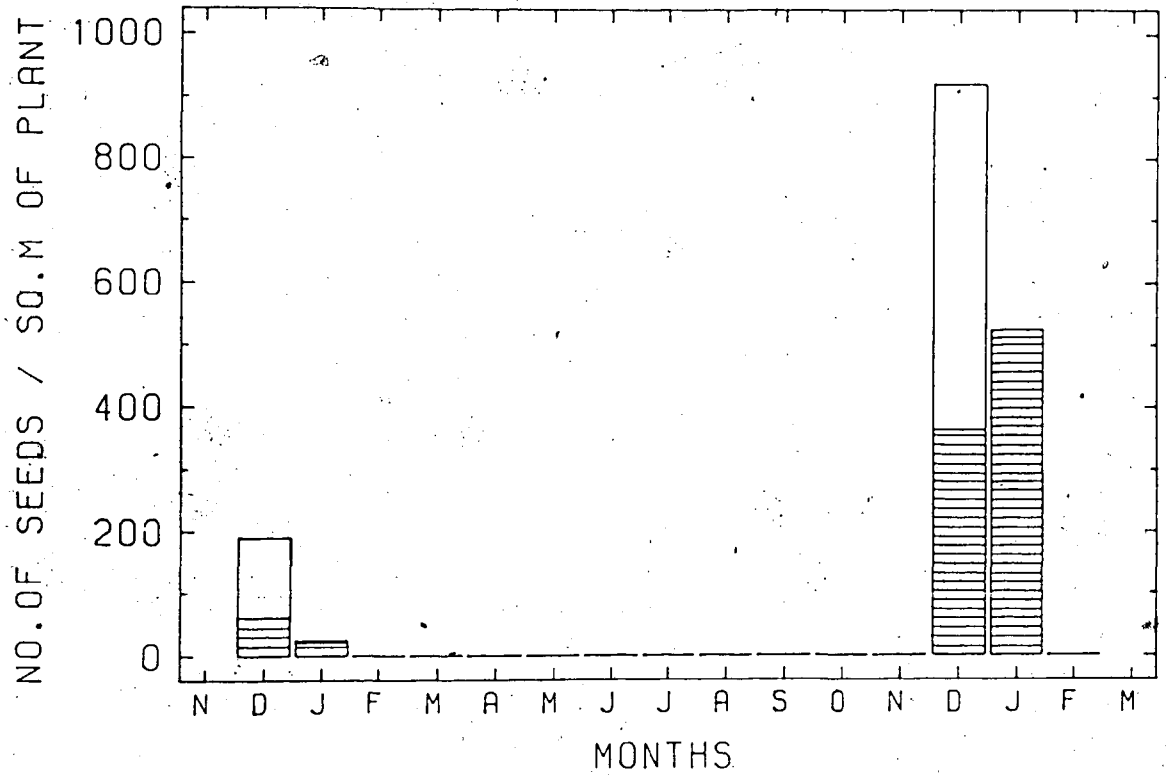
FIG. 3.5. Seed production of A. longifolia between December 1980 and January 1982, expressed as the number of seeds m^{-2} of plant, from seeds collected in traps and classified as whole (□) or empty (▤).

Table 3.1   Summary of flower and seed production in <u>C</u>. <u>monilifera</u> in 1980 and 1981

Parameter measured	1980	1981
Ray florets/inflorescence	12.2 + 0.1*	– **
Seeds/inflorescence	6.6 + 0.3	– **
Seeds/ray florets (%)	54 + 2	– **
Whole seeds m^{-2} of trap	4450 + 750	3900 + 660
Open seeds m-2 of trap	1520 + 450	540 + 190
Viability of whole seeds (%)	80	84
Viable seeds/plant	11036	10156

* S.E. mean   ** not measured

There were no significant differences between the number of seeds near the edge and the centre of plants (t-test, P = 0.28).

Table 3.2 Summary of flower and seed production in
A. longifolia in 1980 and 1981

Parameter measured	1980	1981
Flowers/spike	48 ± 0.6*	-**
Spikes/branch	152 ± 16	-**
Flowers/branch	7300	-**
Plants with pods (%)	35.0	96.7
Pods/branch	4.2 ± 2.1	77 ± 10
Whole seeds/pod	3.5 ± 0.2	4.1 ± 0.3
Whole seeds with parasites (%)	34 ± 5	15.2 ± 2.5 (early Dec) 22.3 ± 3.0 (late Dec)
Viability of whole seeds in traps (%)	65	84 (early Dec) 77 (late Dec)
Viable seeds m^{-2} of trap	33 ± 6	556 ± 125 (Dec) 12 ± 3 (Jan)
Viable seeds/plant	100	1700

* S.E. mean   ** not measured

Most seeds dropped late in the season were predated or non-viable (Fig. 3.5). There were no significant differences between the number of seeds near the outside and centre of plants (t-test, P=0.39). Mean plant size was 3.0 m^2 which was used in the estimation of viable seeds per plant.

3.1.4 Discussion

The abnormally dry conditions in 1980 probably contributed to the low seed production of A. longifolia in that year compared to 1981 (seed production differed by a factor of 17 between years). However, there was little difference in seed production characteristics of C. monilifera between the two years.

Flowering and seed production of C. monilifera was spread over a longer period of the year and total levels of seeds set were much higher than A. longifolia.

Some predation, particularly of A. longifolia seeds, may have occurred in the seed traps so that seed fall may have been underestimated. Seed numbers obtained from pod counts of A. longifolia in 1981 were higher than those from the seed traps but some predation also occurred between the time of pod counts and seed fall. However, even after such allowances are made, viable seed production of C.monilifera was some 10 times that of A. longifolia.

In order to investigate the predation and removal of seeds produced on plants, the figures obtained in this section were analysed more fully in the following.

3.2 Seed predation and dispersal from plants
3.2.1 Introduction

As discussed earlier in this chapter, predation is likely to limit the realisation of the potential of plants especially in their natural habitat. In South Africa, numerous predators limit the growth and reproduction of C. monilifera including a defoliating chrysomelid, a stem-boring cerambycid, a root and crown-boring buprestid, a cecidomyid gall-former which stunts plants, an eriophyid mite in young growth, a rust and a tephritid fly (Mesoclanis magnipulpis and M. dubia) which can destroy up to 70 percent of the seeds (Munro 1950, S. Neser, personal communication 1979). The only seed predation reported in Australia of

C. monilifera has been by red-wing starlings (Wheeler 1964) and by ants and rabbits (Parsons 1973) but in neither case were quantitative data presented.

The numbers of seeds produced by A. longifolia in Australia are reduced by predators such as gall-wasps (New 1979), lepidopteran larvae (van den Berg 1977), coleopteran larvae (Auld & Morrison 1981), ants (Majer 1978) and birds (N. Ford, personal communication, 1980).

Accordingly, I first analysed quantitative data on the amount of predation of seeds on plants of C. monilifera and A. longifolia obtained from section 3.1.

3.2.2 Methods

The amount of predated seed of C. monilifera was obtained from the numbers of open seeds recovered (as pericarps) from covered and uncovered seed traps in section 3.1. Entire seeds removed from plants or traps were calculated in section 3.2.3.1. Only uncovered traps were used for A. longifolia.

3.2.3 Results
3.2.3.1 C. monilifera

The use of uncovered and covered traps allow an estimate of the fate of the seeds since the following equations must hold:

$$P = W_u + H_t + H_p + F + T \quad \dots\dots\dots\dots\dots\dots(1)$$

and, in the case of covered traps,

$$P = W_c + H_p + F \quad \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots(2)$$

where P = total seed production
W_u = whole seeds in uncovered traps
W_c = whole seeds in covered traps
H_t = husks or pericarps from seeds predated in traps
H_p = husks or pericarps from seeds predated on plants
F = whole seeds removed from plants
T = whole seeds removed from traps.

Estimates are available for the following (as rounded numbers/plant):

$$P = 20700 \pm 2400$$
$$W_u = 12600 \pm 1600$$
$$W_c = 13300 \pm 1700$$
$$H = H_t + H_p = 3100 \pm 500$$
$$H_p = 2900 \pm 400$$
$$H_t = 200$$

This leaves F and T to be estimated.
From equation (2),

$$F = P - W_c - H_p$$
$$= 4500$$

and, subtracting (1) from (2),

$$W_c - W_u = H_t + T$$
$$T = W_c - W_u - H_t$$
$$= 500$$

Wide confidence limits imply that these results could be misleading, but the similarity in the number of husks in covered and uncovered traps shows that H_t is small. Also the small difference between W_c and W_u implies that T is also small, ie. predation from the traps was small.

The fate of seeds thus fell into three categories (values are given in terms of rounded percentages):

(a) 20% of seeds were taken whole from plants;
(b) 15% of seeds were eaten on plants and husks dropped; and
(c) 65% of seeds fell to the ground.

Predation (b) was mainly by parrots, usually crimson rosellas (Platycercus elegans), which were observed feeding on the seeds on the plants. The highest such predation, in terms of percentages of pericarps to whole seeds, was in February 1981 and 1982 (Fig. 3.4). Predation (a) was mainly by pied currawongs (Strepera graculina) which regurgitated the seeds elsewhere and so represented a major method of dispersal. Piles of such seeds were found under 'E. botryoides trees located behind the frontal dunes. There was a mean of 720±245 seeds per pile (n=20). There was no significant reduction in viability of these seeds compared with those on the parent plants (one hundred

seeds from each category were tested and the numbers germinated compared in a t-test (P=0.65)). Seedlings of C.monilifera were also observed under E. botryoides.

3.2.3.2 A. longifolia

Parasitised seeds contained either the hymenopteran larvae, Trichalogaster longifolia, or larvae of the coleopteran weevil, Melanterius sp., the activity of which would eventually kill the seeds. Such seeds amounted to 50 per plant in 1980 (a year of low seed production) and 500 per plant in 1981. These represented 34% in 1980 and 19% in 1981 of the total number of apparently whole seeds.

The level of bird predation, mainly by silvereyes (Zosterops lateralis), was high in seed collected late in the season (in January) and 96% were empty (Fig. 3.5). Predation was estimated only in uncovered traps so that detailed analysis as with C. monilifera was not possible.

Seed production was also affected by predation. Five out of 20 plants being measured for shoot growth (Ch. 6) had some stems predated in 1981 and no seeds were set on these stems. Larvae of the blue diamond beetle (Chrysolofus sp.) and a longicorn beetle (Uracanthus sp.) were found inside these stems.

3.2.4 Discussion

Removal of 20% of whole seeds of C. monilifera by currawongs represents a major method of dispersal at least in the study area. In other areas, cattle and emus have also been observed to disperse seeds of C. monilifera in their droppings. No dispersal of A. longifolia seeds predated on the plants was observed, presumably because of destruction of the seeds by different agents.

Further predation can occur after seed fall so that relevant experiments were conducted and reported in the next section.

3.3 Predation after seed fall

3.3.1 Introduction

Ants are common post-dispersal predators of seeds of many species in Australia but do not generally cause extreme depletion of seed populations. For example, Rogers (1974) found only 2% of the available seed biomass removed by ants, but A.B. Wellington (personal communication, 1980) found most fallen seeds of the mallee, Eucalyptus incrassata, quickly taken by ants (seeds had a half-life of 1.7 days).

Seed predation can be advantageous in cases where some seeds are dispersed while retaining their viability. This occurs with C. monilifera ssp. monilifera in Australia where birds, ants and rabbits aid in dispersal of this sub-species (Parsons 1973). In the case of ant dispersal, A. longifolia has been listed as a myrmecochorous species in Australia (Rice & Westoby 1981). I carried out experiments to determine the extent of predation after seed fall and the relative effects of different predators.

3.3.2 Methods

Several experiments were conducted between October 1980 and January 1982 (Table 3.3) in order to determine:

(i) the fate of single seeds on the soil surface

(ii) the relative amounts of predation of clumps of seeds by
     birds, small animals and ants.

Some of the experiments were done at different times of the year to compare predation at these times.

The "row" experiment was located in the open on the fore-dune, mid-dune and swale. Each seed was marked with a small spot of nail varnish on the side resting on the sand. Counts were made after one day and then weekly for 3 weeks and seeds divided into the following categories: undisturbed, moved but still on the sand surface, buried or lost.

In the other experiments, clumps of the two species were placed separately on trays made of particle board, with the surface covered with glued-on sand. The trays had a circular indentation, 4 cm diameter, and 0.4 cm deep, holding the seeds in the middle. The trays were partly buried so that the top was level with the sand surface except for the "stake" experiment where half the trays were placed on top of 1 m high stakes.

Table 3.3 Summary of seed predation experiments

Experiment	Date Commenced	Duration	Seeds/ species/ replication	Repli- cations	Seed arrangement
"Row"	Oct 1980	3 weeks	150	3	5 cm apart in rows
"Tray"	Oct 1980	2 weeks	25	8	Clumped on trays on sand
"Stake"	Nov 1980, Apr 1981	4 weeks	25	8	Clumped on trays on sand or on stakes
"Ant"	Jan 1982	4 weeks	50	8	Clumped on trays on sand c. 2 m from ant nests

FIG. 3.6.   Arrangement of treatments in the 'ant' experiment,
            2 weeks after commencement, showing from left to
            right, top row, treatments 4 (wire mesh + Tanglefoot),
            1 (control) and 3 (wire mesh); bottom row, treatment
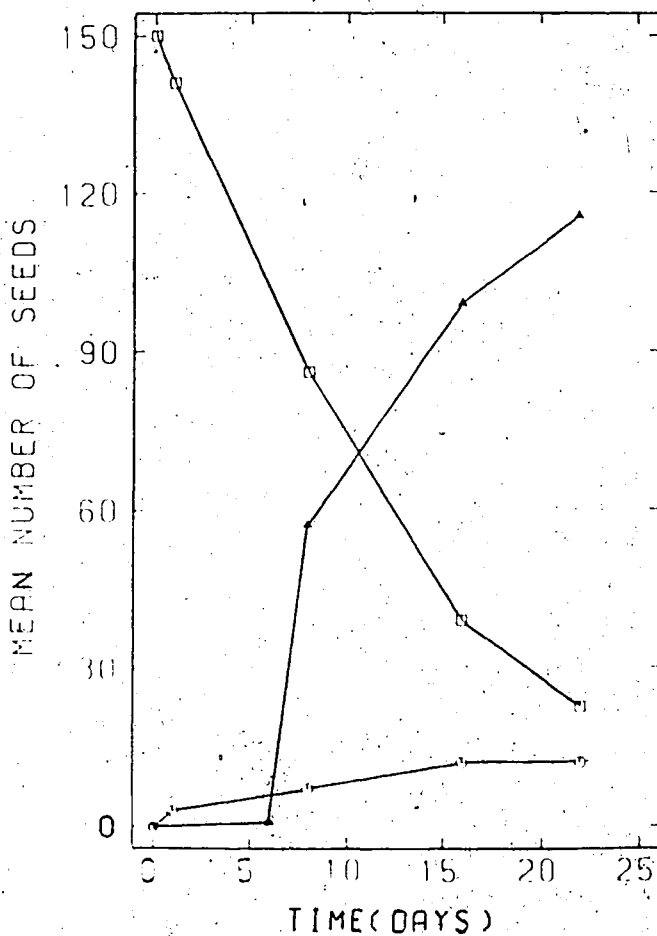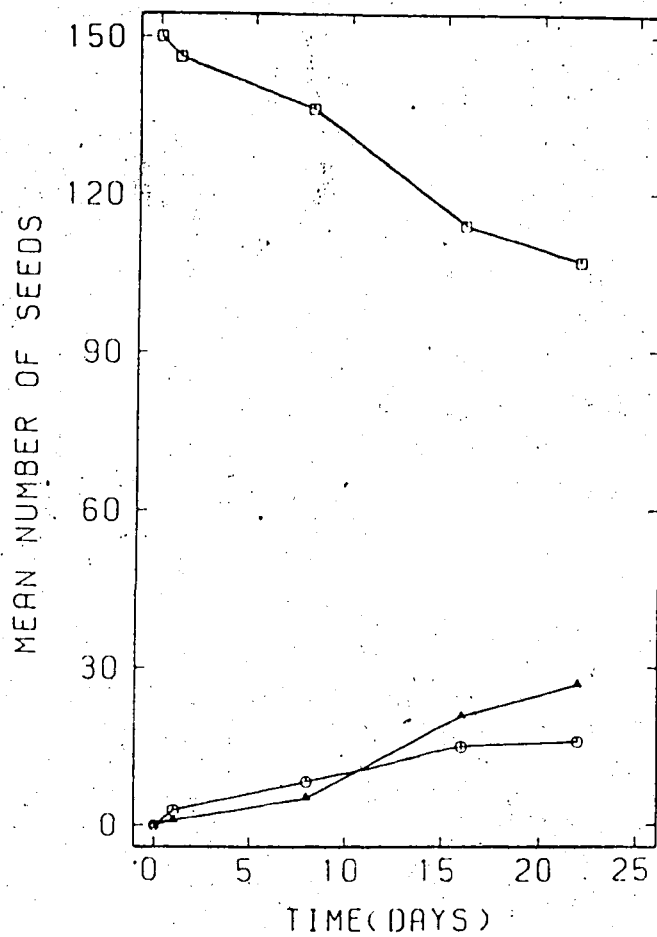   2 (Tanglefoot). Note predated seeds in treatments 1
            and 2.

FIG. 3.7. Mean number of seeds of C. monilifera (top) and A. longifolia (bottom), classified as being on the soil surface (□), buried (O) or missing (Δ) at various times up to 22 days after the start of the 'row' experiment.

Trays were unprotected in the "stake" experiment. In the "tray" experiment, the following treatments were used:

1. Control;

2. Surface of tray around the indentation covered with "Tanglefoot" (a sticky substance designed to exclude crawling insects);

3. Tray covered by an 8 cm high cage made of wire-netting, 1.5 cm mesh; and

4. Tray covered by a similar cage, 5 cm mesh.

In the "ant" experiment, treatments 1, 2 and 3 above were repeated but treatment 4 had a 1.5 cm mesh cage as well as "Tanglefoot" on the tray (Fig. 3.6). Counts were calculated as percentages and were arcsine transformed (Sokal & Rohlf 1969, p. 386) before analysis of variance. The untransformed counts are shown in the results.

3.3.3 Results
3.3.3.1 "Row" experiment

Results were similar in the three locations and mean figures are given in Fig. 3.7. The undisturbed and moved categories were combined because of the effect of wind in moving seeds slightly.

In order to more fully describe the processes of predation and burial, a model was fitted to the observed values in this experiment. Values were derived for a "decay constant" which consists of the proportion lost per unit time (m) and the proportion buried per unit time (b). Then the change in seed number with time is:

$$dN/dt = - N (m + b)$$

and so

$$N = N_O \, e^{-(m + b)t} \quad \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots(1)$$

where N = number of seeds remaining at time t

and N_O = original number of seeds (150).

Then, if M = number of seeds lost

$$d\,M/dt \;=\; m\,N$$

$$=\; m\,N_o\,e^{-(m+b)t} \qquad \text{from (1)}$$

$$\therefore\; M \;=\; \int_o^t m\,N_o\,e^{-(m+b)t}$$

$$=\; \left[-m\,N_o\,\frac{e^{-(m+b)t}}{m+b}\right]_o^t$$

$$=\; \frac{m\,N_o}{m+b}\left[1 - e^{-(m+b)t}\right] \qquad\dotfill(2)$$

Similarly, if B = number of seeds buried,

$$B \;=\; \frac{b\,N_o}{m+b}\left[1 - e^{-(m+b)t}\right] \qquad\dotfill(3)$$

The parameters m and b in equations (2) and (3) may be obtained as follows:

An estimate of u, where u = $m + b$, may be obtained from the slope of the regression of ln N against time.

> For C. monilifera, u = 0.015
> and A. longifolia, u = 0.085

An estimate of r, where r = b/m, may be obtained from the final counts in Fig. 3.7, since dividing equation (3) by (2) gives B/M = b/m.

> For C. monilifera, r = 0.593
> and A. longifolia, r = 0.104

Then, b = $\left[\, r/(1 + r)\, \right]$ u

> For C. monilifera, b = 0.006
> and A. longifolia, b = 0.008

and

$$m = \left[\, 1/(1 + r)\, \right] u$$

> For C. monilifera, m = 0.009
> and A. longifolia, m = 0.077

These values may then be substituted in equations (2) and (3). The fitted values correspond closely to the final counts in Fig. 3.7. The above parameters show that A. longifolia has more than eight times the rate of disappearance of surface seed compared to C. monilifera (7.7% per day and 0.9% per day respectively). The rate of seed burial was low and similar in both species (0.8% and 0.6% per day).

3.3.3.2 "Tray" experiment

There was significantly less predation of C. monilifera when it was protected by either type of wire mesh and of A. longifolia protected by fine wire mesh (Table 3.4). There was a significantly higher level of predation of A. longifolia than C. monilifera in all treatments.

Table 3.4 Mean number of whole seeds out of 25 each of C. monilifera
and A. longifolia remaining after 2 weeks

Treatment	C. monilifera	A. longifolia
1 - Control	5.8 Aa	0 Ab
2 - Tanglefoot	5.8 Aa	0 Ab
3 - Wire mesh (1.5 cm)	24.4 Ba	17.4 Bb
4 - Wire mesh (5 cm)	24.2 Ba	0 Ab

Table 3.5 Mean number of whole seeds out of 25 each of C. monilifera
and A. longifolia remaining after 4 weeks in either
November or April

Treatment	C. monilifera	A. longifolia
	November	
Stakes	12.0 Aa	0.25 Ab
Ground	10.5 Aa	0.1 Ab
	April	
Stakes	21.0 Ba	1.0 Ab
Ground	19.8 Ba	1.0 Ab

Table 3.6 Mean number of whole seeds out of 50 each of C. monilifera
and A. longifolia remaining after 4 weeks

Treatment	C. monilifera	A. longifolia
1 - Control	3.3 Aa	0 Aa
2 - Tanglefoot	9.0 Aa	0 Ab
3 - Wire mesh	48.0 Ba	·0 Ab
4 - Wire mesh + tanglefoot	44.5 Ba	40.0 Ba

3.3.3.3 "Stake" experiment

There was a significantly lower level of predation of C. monilifera in April than November (Table 3.5). At neither time were there significant differences between levels of predation of seeds on the ground or on stakes of both species. There was a significantly higher level of predation of A. longifolia than C. monilifera in all treatments.

3.3.3.4 "Ant" experiment

The level of predation of C. monilifera was significantly lower when it was protected by fine wire mesh (Table 3.6). All seeds of A. longifolia were missing after 4 weeks except where protected by wire mesh and "Tanglefoot".

3.3.4 Discussion

Similar levels of seed burial of C. monilifera and A. longifolia (about 13% and 18% respectively) were observed in the "row" experiment. However, the level of predation of seeds of C. monilifera was lower than that of A. longifolia in all experiments. The sometimes high levels of predation of C. monilifera seeds ("tray" and "ant" experiments) may have been due to their being in clumps and so more accessible to predators, since loss of isolated seeds was low (20% over the period of the "row" experiment).

Pericarps of C. monilifera were observed in the "tray" experiment which were similar to those seen after predation by parrots. This was not unexpected because of activity of such birds in the area at the time of this experiment (spring).

Ants were less important as predators of C. monilifera seeds since "Tanglefoot" made no significant difference to the numbers lost although there was a trend towards higher predation levels of unprotected seeds near active ant nests ("ant" experiment).

On the other hand, the contribution of ants to removal of seeds of A. longifolia (when protected by fine bird wire) varied from 30% in the "tray" experiment to 100% in the "ant" experiment. The high predation in the latter experiment may have been due to its location near active ant nests. Alternatively, ant predation may be higher at the time of seed fall (December to January) when the "ant" experiment was initiated than in October ("tray" experiment). Since

A. longifolia is a myrmecochore (Rice & Westoby 1981), it is surprising that no seedlings were observed on ant middens, but seeds may become buried too deeply for subsequent seedling emergence. I observed that ants removed just as readily the funicle and aril, when separated, as the entire seed. Ants may thus utilise only the funicle and aril and discard the rest of the seed which may then be taken by other predators.

The lower level of predation in April compared with November in the "stake" experiment corresponded to the low amount of predated seed of C. monilifera in traps in April (24%) (Fig. 3.4). Similarly, the high level of predation of seeds of C. monilifera of 88% during February in the "ant" experiment corresponded to the level of opened seeds (79% and 81% of the total) in traps in February 1981 and 1982 respectively. However, absolute numbers of predated seeds of C. monilifera were not high in February as total seed drop was lowest between November and February (Fig. 3.4).

Birds or small animals were mostly responsible for the removal of 100% of seeds of A. longifolia in the "tray" experiment but their relative effects on seeds of either species could not be separated in the "stake" experiment. An additional predator known to feed on Acacia seeds, leaving only the seed coat, is the nigger-bug (Cydnidae sp.) which was observed under the litter around mature plants.

Predation of A. longifolia seeds prior to their fall by weevils and wasps, coupled with large losses after seed fall by ants and birds or small animals are greater than that of C. monilifera. Further, predation by currawongs of C. monilifera seeds prior to their fall (section 3.2) is important in that seeds remain intact and so enables plant spread and invasion of new areas. Predation should be quantitatively less detrimental to the seed pool of C. monilifera than A. longifolia because of the higher numbers of seeds of C. monilifera produced. This led to an investigation of the actual levels of such seed pools in the next section.

3.4 Soil seed pool
3.4.1 Introduction

The importance of viable seed, often in large numbers, buried in the soil has long been recognised in agriculture in connection with weed control (Duvel 1902, Brenchley& Warrington 1930, Chippendale & Milton 1934, Kropac 1966, Roberts 1967). However, it is only comparatively recently that much attention has been paid to the role

of seed "banks" in natural plant communities as opposed to agricultural ones (Roberts 1981).

Barbour & Lange (1967), working in natural communities containing A. longifolia var. sophorae in Australia, failed to find seeds of that species in soil under established plants. However, others have warned that the seed pool does not necessarily reflect the present vegetation, in some cases due to low seed inputs and rapid loss from the surface seed bank (Kellman 1974, Whipple 1978, Thompson & Grime 1979). These reasons may be applicable to A. longifolia in Australia since high densities (7600 ± 2500 m^{-2}) of seeds of this species were found in the soil in South Africa (Milton & Hall 1981).

A similar discrepancy exists between Australia and South Africa in values for seed pools of C. monilifera ssp. monilifera. In Australia, over 2500 whole seeds m^{-2} have been found (D.W. Lane, personal communication) while only 100-300 whole seeds m^{-2} were recorded in South Africa (Milton 1980). Seed production was apparently high in South Africa but large numbers of open or fragmented seeds ($4000 - 6000$ m^{-2}) were found (Milton 1980), due either to predation, germination or decay, with predation probably the dominant factor (S. Neser, personal communication).

Although data had been obtained on seed production of C. monilifera ssp. rotundata and A. longifolia (section 3.1), it is apparent that the size of the viable seed pool is determined also by seed longevity and the numbers of seeds germinating, predated or otherwise lost. Hence there was a need to determine the size and seasonal variability of the soil seed pool of both species at several times in the year.

3.4.2 Methods

Sampling of the seed pool of C. monilifera was carried out at two-monthly intervals from October 1980 until March 1982 and of A. longifolia in January, April and September 1981 and January and April 1982. Initially areas sampled were located at the centre of a plant and then at 1 m intervals towards the outside of the plant and for a further 4 m into the open. Subsequently only an area under the canopy and 1 m in from its edge was sampled. In each case, an area of 0.5 m x 0.5 m was sampled to a depth of 10 cm, under six plants each of C. monilifera and A. longifolia. Each sample was sieved (1.5 mm mesh), sub-sampled (25% of the total by weight), seeds separated from litter and organic matter by hand and divided into whole (apparently

normal), empty or open and sterile (shrivelled) seeds of <u>C. monilifera</u>
and whole and empty seeds of <u>A. longifolia</u>.

Further samples were taken at the end of September, October,
November and December 1982 with a 3.65 cm diameter sampling tube to
determine the number of seeds of <u>C. monilifera</u> at depths of 0, 0-2,
2-4, 4-6, 6-8 and 8-10 cm. Samples were obtained from under 20 plants
each time and sorted in a similar manner to those described above
except that sub-samples were not taken.

3.4.3 Results

There were only small differences in total seed numbers between
samples under the plant canopies but a marked reduction beyond the
edge of the plants (Table 3.7).

The numbers of apparently normal seeds of <u>C. monilifera</u> were
lowest in April while open or empty seeds were highest at that time
(Fig. 3.8). Numbers of both whole and empty seeds of <u>A. longifolia</u>
were highest in January (Fig. 3.8) but larger numbers of whole seeds
were observed on the soil surface in December, at the time of seed
fall. Most seeds of <u>C. monilifera</u> were also found on the soil surface
and no viable seeds were recovered from a depth of 4-10 cm (Table
3.8).

3.4.4 Discussion

The small spread of seeds beyond parent plants was probably
because of the weight of individual seeds (33+2 mg for <u>C. monilifera</u>
and 40+1 mg for <u>A. longifolia</u>). However, plants sampled were on
comparatively even ground so that a wider pattern of seed dispersal
might be expected on steeper dune slopes.

The total number of seeds of <u>C. monilifera</u> found during the year
was comparatively constant, although there was a slight decline
between the beginning and end of the sampling period. The reason for
this was not investigated but may have been due to variability in seed
set or predation. The decrease in whole seed numbers in April
(Fig. 3.8) was probably because some seeds in this category germinated
in autumn and some had died, contributing also to the rise in open or
empty seeds at this time. Subsequently the numbers of whole seeds
rose because of the large seed input in June (section 3.1).

Table 3.7 Number of soil seeds m^{-2} of quadrat of <u>C</u>. <u>monilifera</u> in October 1980 and <u>A</u>. <u>longifolia</u> in January 1981 at various distances from plant centres

Position	<u>C</u>. monilifera			<u>A</u>. longifolia	
	Whole	Open	Sterile	Whole	Open
Centre	5813 + 964*	6484 + 910	1706 + 66	17 + 2	45 + 7
Between centre and edge	5507 + 777	6379 + 605	2059 + 480	18 + 3	50 + 9
Edge	3403 + 507	7054 + 838	1630 + 215	20 + 3	49 + 8
Edge + 1 m	100 + 20	360 + 90	10 + 3	0	0
Edge + 2 m	48 + 9	126 + 33	11 + 3	0	0
Edge + 4 m	0	11 + 3	0	0	0

* S.E. mean

Table 3.8. Number of viable seeds m^{-2} of quadrat of *C. monilifera* from September to December 1982 at depths of 0, 0-2 and 2-4 cm

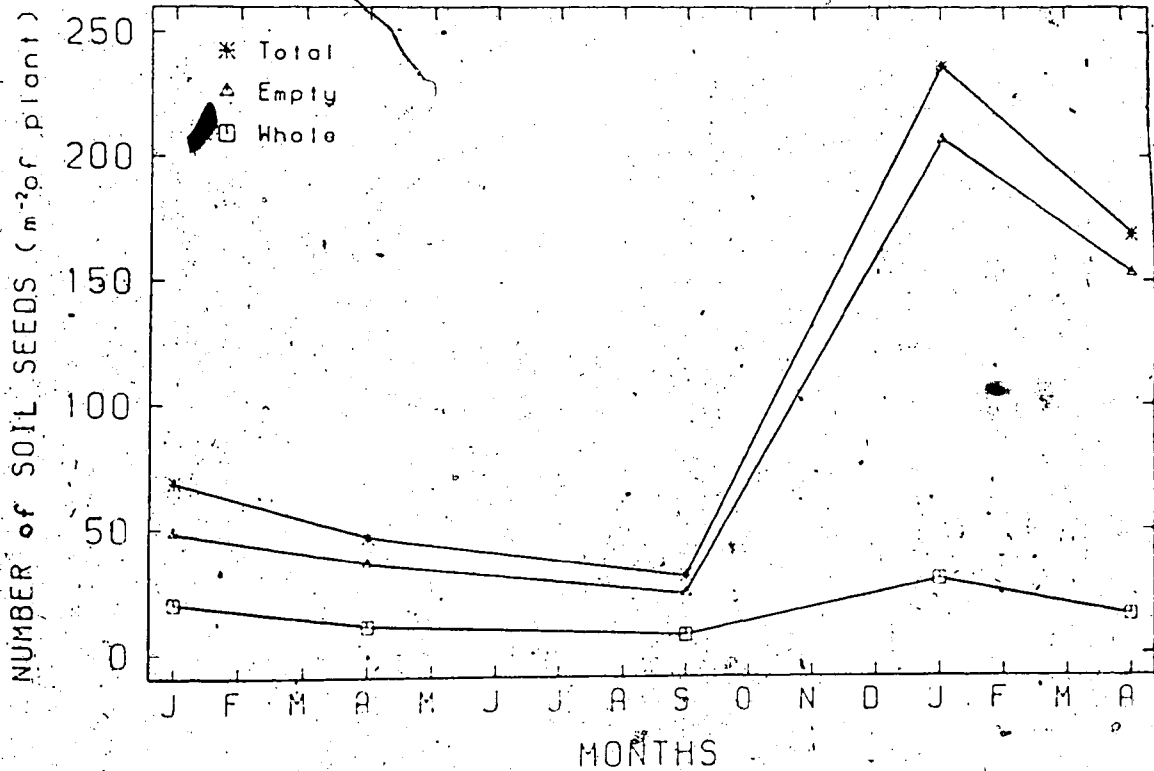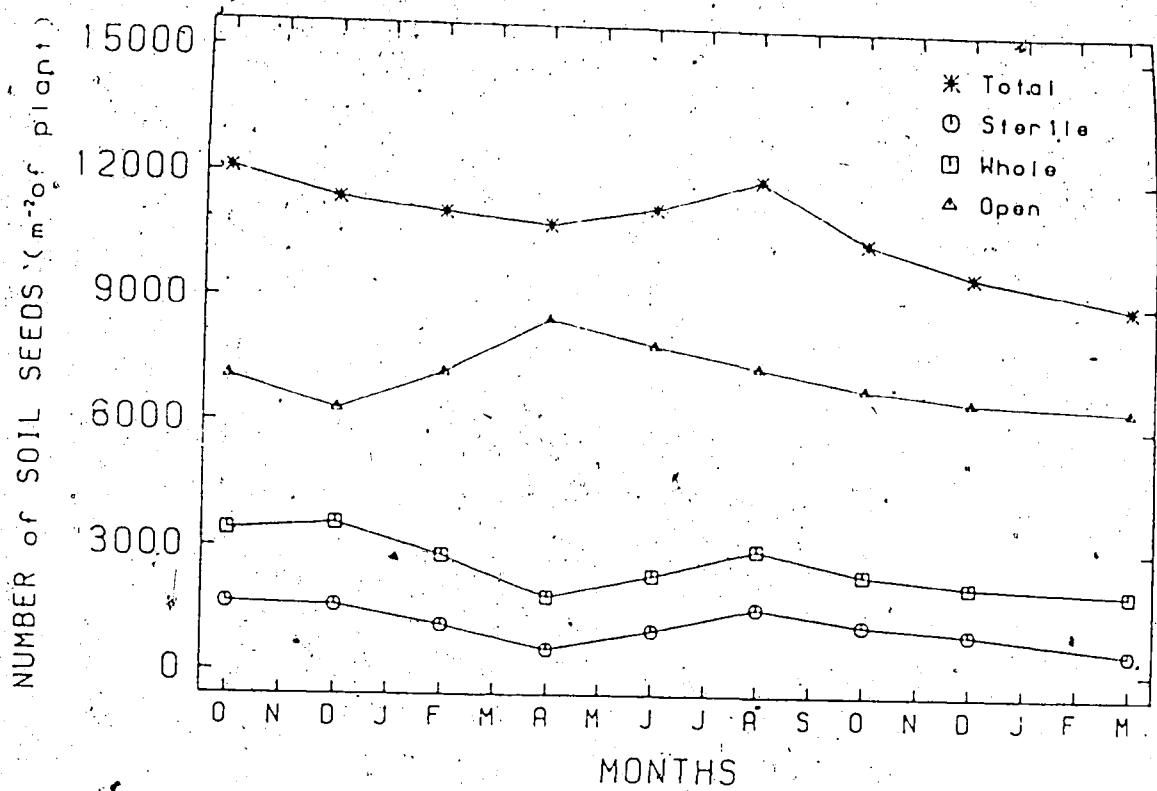| Month	0	0-2 cm	2-4 cm	Total
September	1911 ±438*	255 ±113	127 ±87	2293
October	1974 ±370	1019 ±442	64 ±64	3057
November	1433 ±281	690 ±216	106 ± 8	2229
December	1452 ±240	540 ±181	42 ±42	2034

* S.E. mean

FIG. 3.8. Number of soil seeds of <u>C. monilifera</u> (top) and <u>A. longifolia</u> (bottom), expressed as numbers m^{-2} of quadrat under the plant canopy.

Soil seed numbers of A. longifolia, at no time very large, were much lower than those recorded for seed fall (section 3.1), apparently due to predation between the time of seed fall and sampling. Despite large differences in total seed output of A. longifolia between 1980 and 1981 (section 3.1), reflected in the numbers of empty seeds, the number of whole seeds was uniform (but low) during the sampling period (Fig. 3.8).

The number of viable seeds of C. monilifera in the seed pool was some 65 times greater than that of A. longifolia because of the comparatively high level of seed production and low level of predation of C. monilifera compared to A. longifolia.

Only 30% of viable seeds of C. monilifera in or on the soil were found buried (see also section 3.3.3.1). Longevity of such seeds is, however, important in the size of the soil pool. This is discussed in the following section.

3.5 Seed longevity
3.5.1 Introduction

It is well known that longevity of seeds varies greatly between different plant species and with the prevailing environmental conditions of storage. Usually, viability of seeds in the field is less than that of those stored in the laboratory. For example, Piggin (1976) found that some seeds of Echium lycopsis (Paterson's curse) were still able to germinate after 6.5 years storage under laboratory conditions but no viable seeds remained after storage for 5 years in the field.

There is evidence that deeper burial in the field leads to greater longevity (Waldrow 1904, Dawson & Bruns 1975, Thomas & Allison 1975). One of the reasons for more rapid depletion of viable seeds in the upper layers of soil is that those near the surface are less likely to be in a state of enforced dormancy and more likely to either lose viability or germinate in situ (Major & Pyott 1966, Taylorson 1972, Stoller & Wax 1973).

Acacia seeds are generally recognised as being relatively long-lived because of their hard, impervious testas. For instance, Cambage (1926) observed that seedlings of Acacia mollissima germinated after ploughing although plants had been absent for 86 years.

Seeds of <u>C.</u> <u>monilifera</u> ssp. <u>monilifera</u> were found to be viable in the field for at least 10 years (Pizzey 1974, Lane 1976). Such longevity is likely to be linked to the ecological behaviour of a particular species so that, for example, in species in which germination is triggered by an infrequent occurrence such as fire, seed longevity is an important adaptation. I decided to compare the seed longevities of the two sub-species of <u>C.</u> <u>monilifera</u> with those of some Australian species which are associated with ssp. <u>rotundata</u> and to attempt to relate these to other ecological characteristics of each.

3.5.2 Methods

Recently harvested, untreated seeds of <u>C.</u> <u>monilifera</u> ssp. <u>rotundata</u> and ssp. <u>monilifera</u>, <u>A.</u> <u>longifolia</u> var. <u>sophorae</u>, <u>B.</u> <u>integrifolia</u> and <u>Albizia</u> <u>lophantha</u> were obtained. Bags made of fibreglass mesh screen were made, with the open end sewn on to a metal ring 20 cm in diameter. These were filled with sieved soil (sand) from the field site at Moruya and placed there at three sites, with the ring at the top of the bag level with the soil surface (Fig. 3.9). The experiment commenced in mid-November 1979 at the same time that natural seed drop of <u>A.</u> <u>longifolia</u> was occurring. Mature plants were at least 5 m away from the seeds so that "leakage" of seed into the plot was minimal (section 3.3).

The seeds (50 of each species) were sown in rows inside the bags at depths of 1, 2, 5, 10 cm (one depth per bag). Provision was made for sampling 3, 6, 12, 18, 24, 36 months after commencement. The experimental design was a completely randomised block, with three replications. Seeds were also placed at the same time in sand in bags in the laboratory. Observations were made at least monthly of emerged seedlings in the field plots.

At each sampling time bags were removed from the field, the contents sieved and the seeds of each species counted to obtain the number remaining out of a possible total of 150 at each depth. The number of empty seeds (either open or obviously empty after squeezing) were also recorded. The remainder were put on moist filter paper in petri dishes and placed in a germination cabinet at 20°C, with a 12-h photoperiod. The number of germinated seeds were counted at regular intervals for 4 weeks. In addition, any seeds of <u>A.</u> <u>longifolia</u> which were ungerminated after 2 weeks, were nicked at the distal end with a scalpel and replaced in the petri dishes for the remaining 2 weeks. Ungerminated seeds were then cut open, any empty ones recorded and the
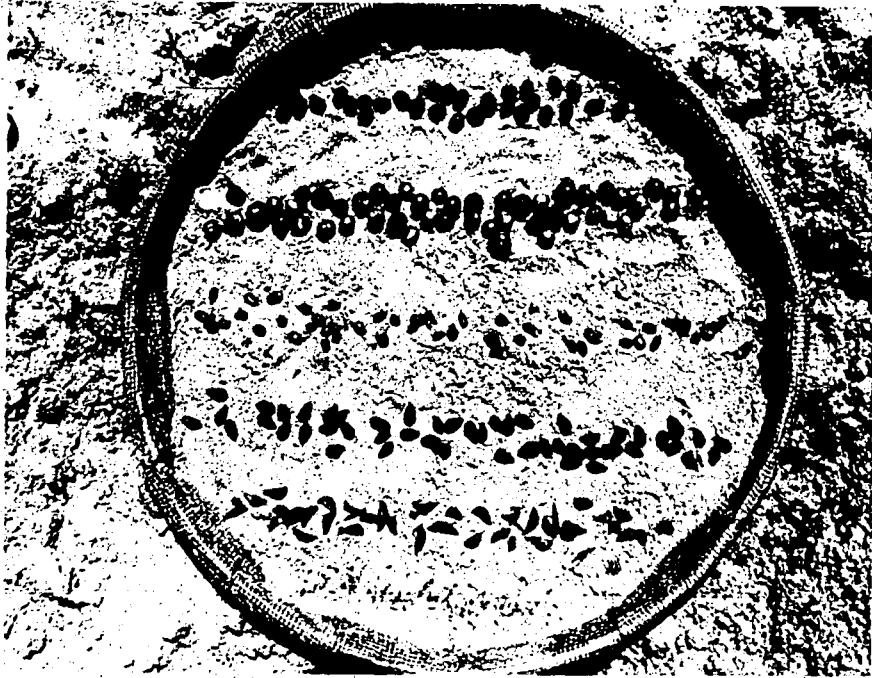
FIG. 3.9. Arrangement of seeds in the longevity experiment in
the 2 cm depth treatment before covering with sand,
showing from top to bottom, Albizia lophantha,
Chrysanthemoides monilifera ssp. monilifera, Acacia
longifolia, C. monilifera ssp. rotundata and Banksia
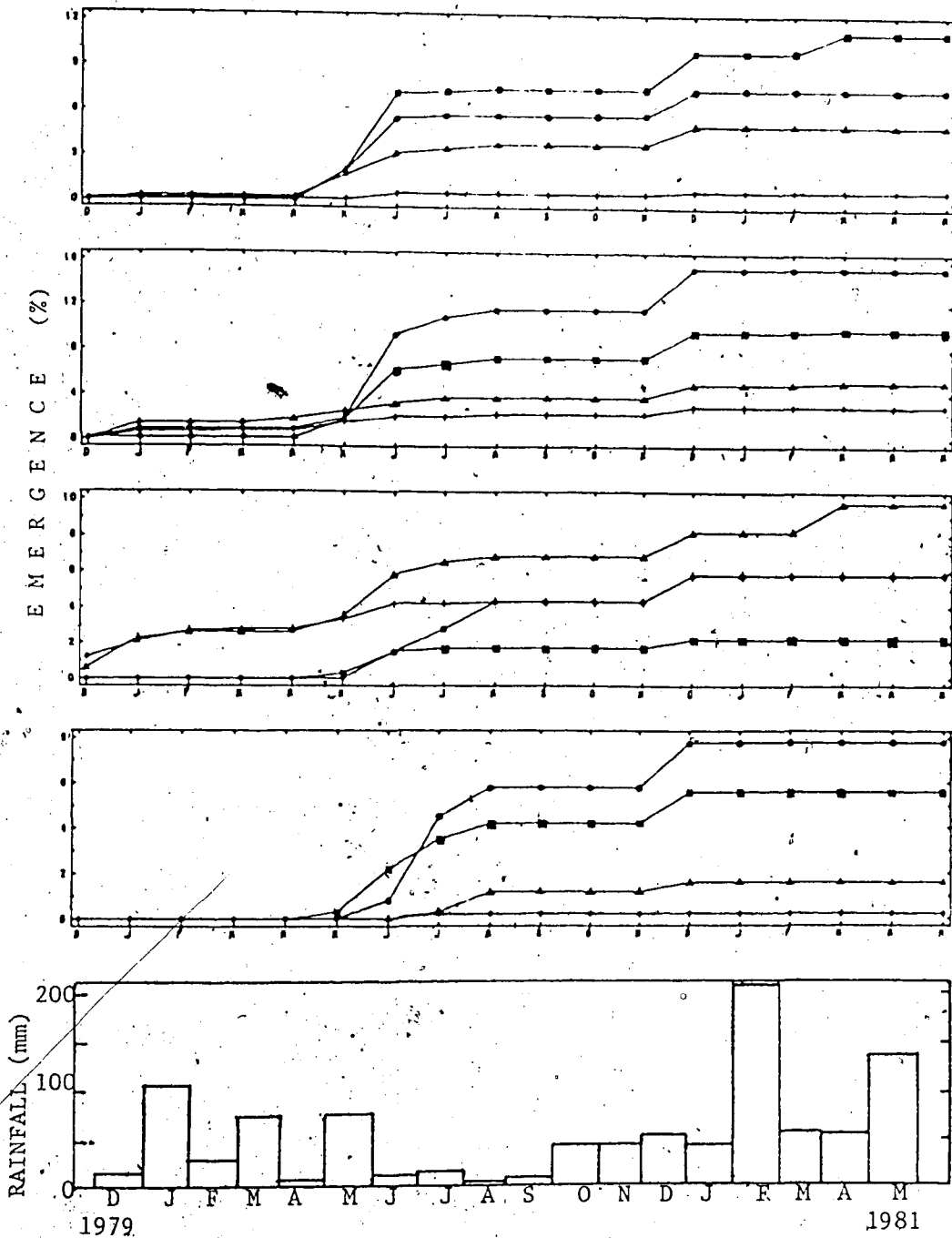integrifolia.

FIG. 3.10: Number of seedlings emerging in the field in the seed longevity experiment, as a cumulative % of the number of seeds, of (from top to bottom) C. monilifera ssp. monilifera, C. monilifera ssp. rotundata, A. longifolia and B. integrifolia from 1 cm (■), 2 cm (●), 5 cm (▲) and 10 cm (+), between December 1979 and May 1981. Monthly rainfall is shown in the bottom figure.

Table 3.9 Mean number of missing seeds out of 50 of <u>A</u>. <u>longifolia</u>
          at five sampling times and four depths of burial

Sampling time	Depth (cm)			
(months)	1	2	5	10
3	15.7 + 8.2*	19.7 + 10.7	25.3 + 5.7	19.0 + 2.6
6	41.0 + 6.0	38.0 + 7.6	22.3 + 2.8	37.7 + 1.2
12	41.7 + 0.9	35.7 + 8.0	39.7 + 4.5	34.0 + 1.0
18	36.5 + 8.5	29.0 + 8.8	24.0 + 4.2	30.7 + 3.5
24	48.7 + 0.7	44.7 + 3.5	46.3 + 1.8	37.3 + 3.2

* S.E. mean

...of four seed lots after 3 to 24 months in the field, ...ed as mean percentages ± standard errors over all soil depths

Species	Emerged (field)	Dormant (enforced)	Dormant (innate)	Missing	Empty	Dead
3 months						
C.monilifera ssp mon	0.5±0.3	10.8±2.1	24.3±6.7	5.0±2.4	40.8± 5.4	18.6±3.7
C.monilifera ssp rot	0.4±0.2	12.0±2.0	13.5±3.8	5.3±4.0	34.0± 4.9	34.8±4.5
longifolia	0.7±0.5	15.3±2.8	11.5±2.4	39.9±6.7	22.8± 4.0	9.8±2.2
integrifolia	0	42.3±3.1	1.0±0.3	27.0±4.1	22.7± 3.2	7.0±0.9
6 months						
C.monilifera ssp mon	1.8±1.6	19.6±3.8	14.9±2.8	14.9±8.0	18.4± 3.0	30.4±7.0
C.monilifera ssp rot	4.7±2.9	6.8±2.0	3.0±1.1	11.3±4.4	65.8± 5.0	8.4±2.8
A. longifolia	4.8±2.9	14.1±3.4	7.2±1.7	69.5±6.2	1.5± 0.3	2.9±0.8
B. integrifolia	0	37.8±4.6	1.0±0.3	36.9±4.8	21.3± 6.3	3.0±1.4
12 months						
C.monilifera ssp mon	4.4±1.7	10.7±3.7	10.3±3.5	14.3±5.2	53.1± 5.9	7.2±1.4
C.monilifera ssp rot	7.2±3.1	1.7±0.7	1.5±0.7	12.8±5.5	74.3±16.0	2.5±0.8
A. longifolia	5.7±2.6	1.9±0.6	9.0±2.7	73.9±4.4	4.0± 1.8	5.5±1.6
B. integrifolia	2.5±1.3	4.2±2.5	0.3±0.2	47.8±6.4	41.5± 7.1	3.7±1.6
18 months						
C.monilifera ssp mon	1.8±0.6	5.3±1.8	8.7±2.3	18.0±8.0	50.5± 7.8	15.7±4.4
C.monilifera ssp rot	6.0±1.9	2.0±0.8	0.8±0.3	17.4±7.0	67.1± 7.6	6.7±2.2
A. longifolia	5.5±1.0	1.2±0.5	6.5±2.4	59.3±6.9	22.2± 4.3	5.3±3.0
B. integrifolia	4.2±1.9	5.1±2.5	0	37.8±8.3	48.0± 7.2	4.9±2.8
24 months						
C.monilifera ssp mon	8.3±3.2	11.3±5.0	2.0±1.1	18.5±8.0	58.7± 7.2	1.2±0.4
C.monilifera ssp rot	6.3±2.5	1.5±0.9	0.5±0.3	28.0±7.4	63.2± 6.5	0.5±0.2
A. longifolia	3.7±1.5	0	6.2±2.5	88.4±3.4	0.5± 0.3	1.2±0.4
B. integrifolia	2.3±1.5	0	0	59.7±6.7	38.0± 7.1	0

others tested for viability with a 0.1% solution of 2, 3, 6- triphenyl tetrazolium chloride.

Each sample could then be divided into the following categories:

1. Emerged in the field.

2. Germinated in the laboratory (enforced dormancy).

3. Dormant (ungerminated but viable or, in the case of A. longifolia, germinated after treatment).

4. Empty (the number in category 1 was subtracted from the total number of empty seeds).

5. Dead.

6. Missing.

Seeds kept in the laboratory were treated similarly except that category 1 was obviously not applicable.

The numbers of dormant seeds (categories 2 and 3) were compared with the numbers in all other categories by a two-way ANOVA of species x depth for each sampling time, using a G-test (Sokal & Rohlf 1969, p. 559).

3.5.3 Results

Most of the A. lophantha seed used had rotted by the first sampling so that this species was disregarded for the rest of the experiment. There was 82 mm of rain in the week after sowing and some field emergence commenced in the first month with all species except B. integrifolia (Fig. 3.10). However, rainfall was low in the following year (Fig. 3.10) and the final percentage emergence was c. 10%. Most emergence occurred from 1 or 2 cm, except for A. longifolia which was greatest from 5 cm (Fig. 3.10).

A. longifolia had the greatest number of missing seeds (Tables 3.9, 10) particularly from the shallowest depth (1 cm) (Table 3.8), although there was no clear relationship between survival and depth. Some shallowly buried seeds were observed to become partially exposed

due to movement of surface sand by wind, but no explanation can be offered for the loss of the deeper seeds.

At the end of the experiment, the percentage of viable seeds of all species was significantly greater after storage in the laboratory than in the field (t-test, P $\leq$ 0.05) (Figs. 3.11, 3.12). In the field, after 18 months with B. integrifolia and 24 months with the other species, the greatest number of viable seeds remaining was at 10 cm (ANOVA, P $\leq$ 0.05) (Fig. 3.13, Table 3.11).

3.5.4 Discussion

The numbers of viable seeds in the soil seed pool represent the potential for continuation of the population or re-invasion should mature plants be removed by fire or some method of control. The depth of burial of these seeds affects their viability and hence is important when stating the seed longevity of a species. Besides other factors, the greater numbers of missing seeds at the shallower depths would also contribute to the shorter longevity observed in viable seed numbers near the soil surface. The high percentage of missing seeds of A. longifolia is probably due to the high predation rates of seeds of this species (section 3.2) which, if anything, could be underestimated here because of the physical barrier of the mesh bags under the surface of the sand.

It is apparent from the results of this experiment that the ecological characteristics of the plants are linked to the longevity of their seeds. Thus the two with the highest seed longevity are C. monilifera ssp. monilifera and A. longifolia. These species also have other important ecological characteristics in common:

1. The adults do not resprout after fire and so are entirely dependent on seed for regeneration after fire.

2. Fire is important for their seed germination. Much denser seedling emergence occurs after a fire due to the breaking of dormancy of "hard" seeds.

3. Both have a comparatively short season or "flush" of flowering, resulting in seed input into the soil over a short period each year. Also A. longifolia is variable from year to year in its seeding pattern and little or none may be produced in a particular year on a given plant.
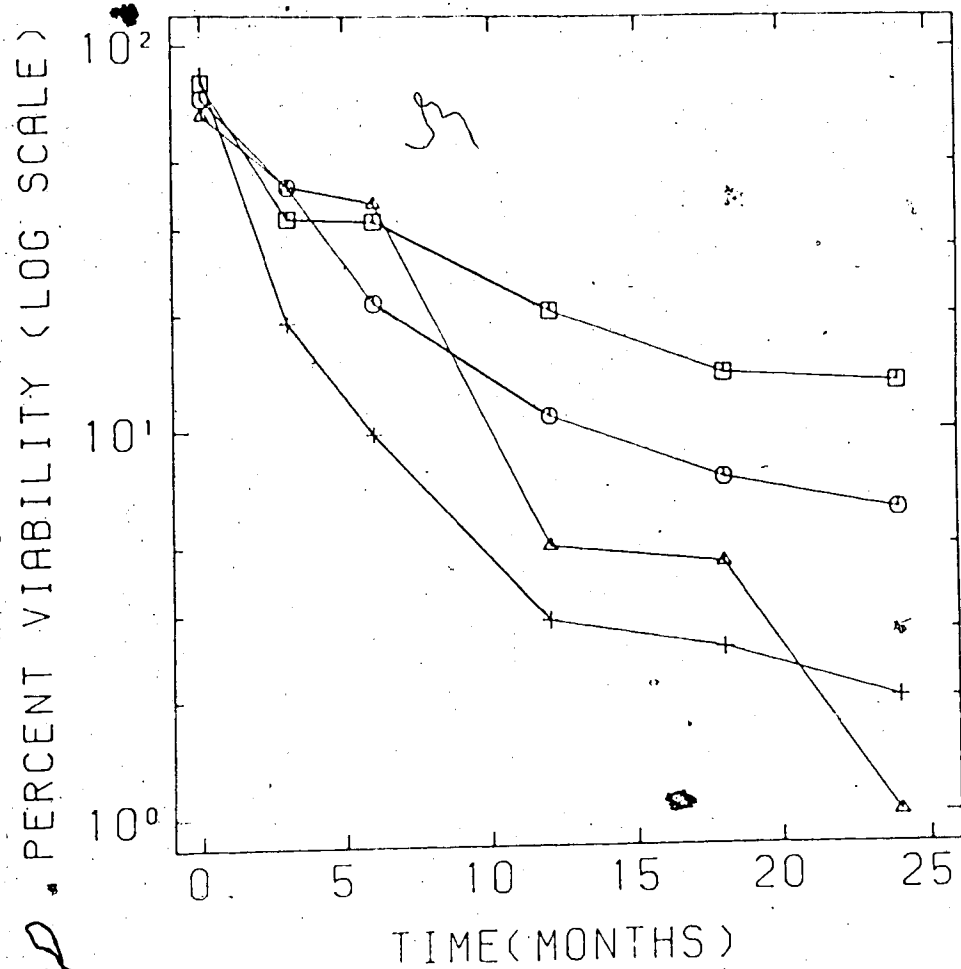
FIG. 3.11. Number of viable seeds, expressed as a % of the total
and as a mean over four soil depths in the seed
longevity experiment, of C. monilifera ssp. monilifera
(□); C. monilifera ssp. rotundata (+), A. longifolia
(0) and B. integrifolia (Δ) (here $10^0 = 0$).
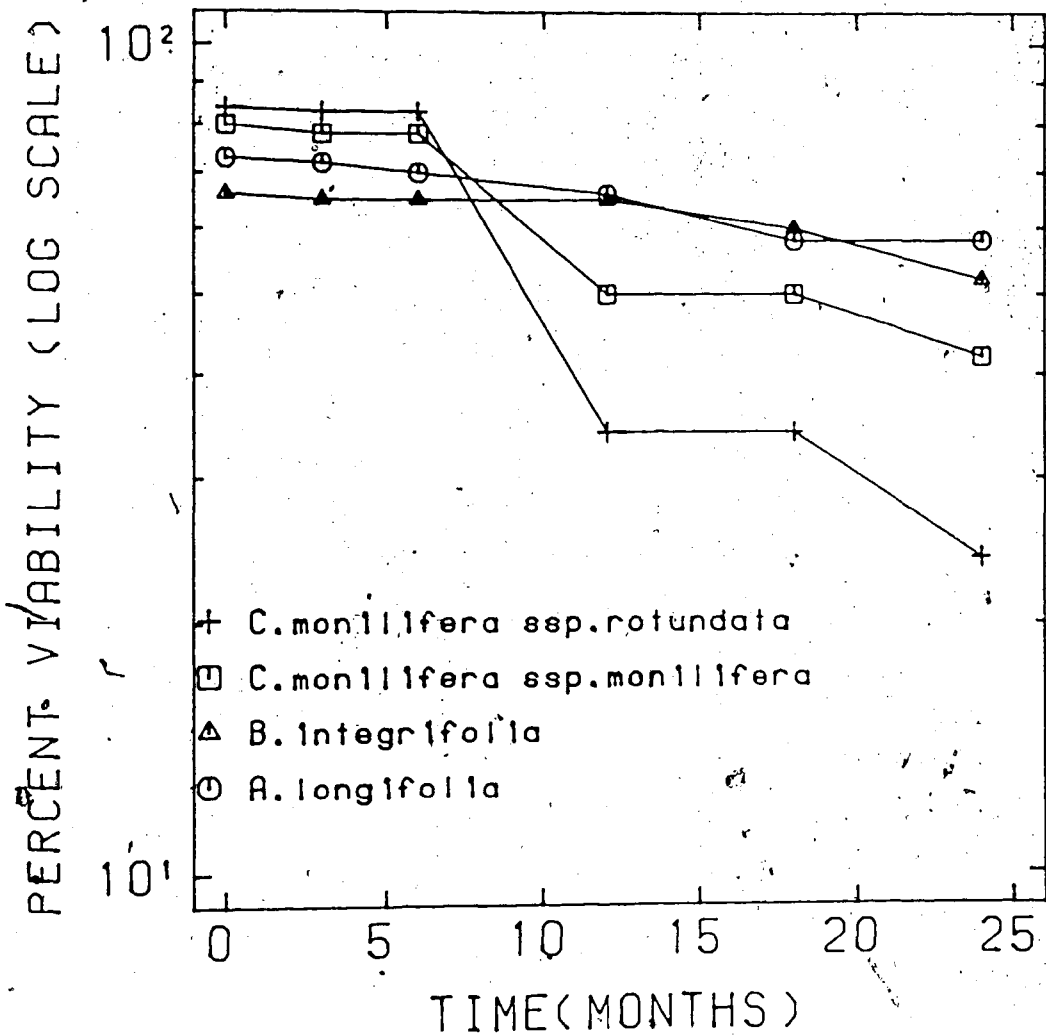
FIG. 3.12. Number of viable seeds of C. monilifera, B. integrifolia
and A. longifolia, expressed as a % of the total, after
various times of storage in the laboratory in the seed
longevity experiment.
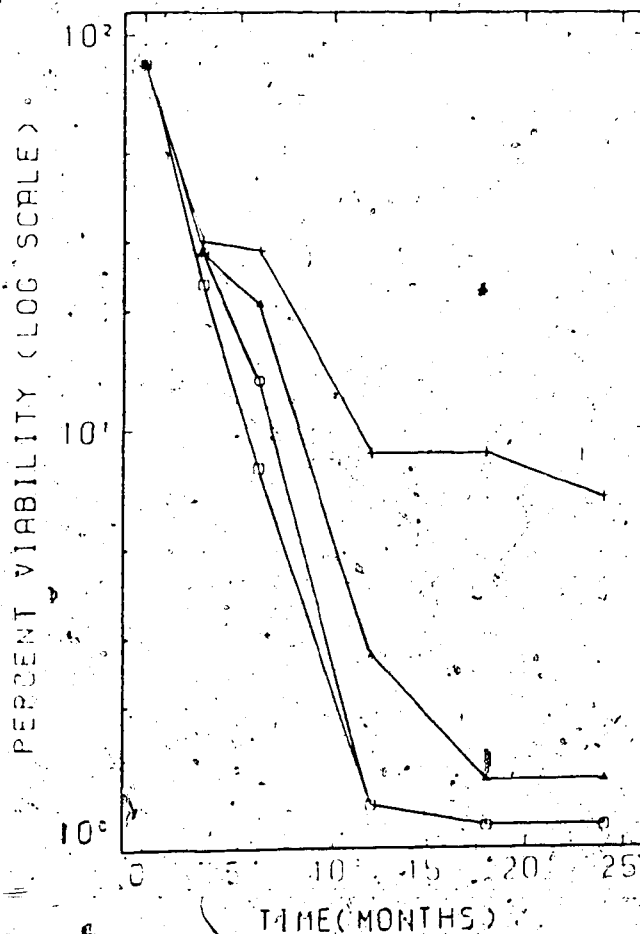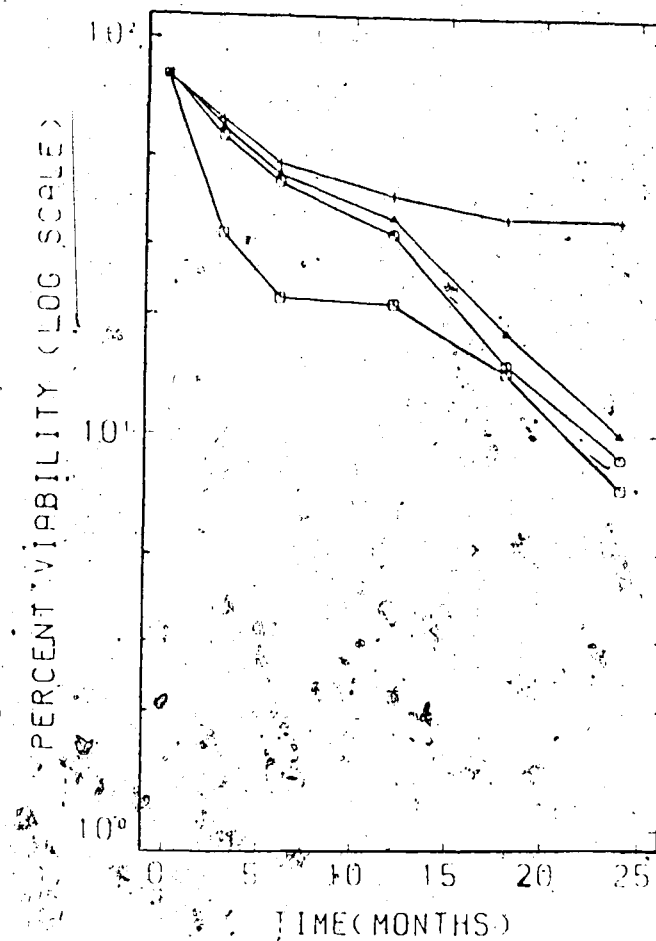
FIG. 3.13 a   Number of viable seeds of C. monilifera ssp. monilifera
(top) and ssp. rotundata (bottom), expressed as a % of
the total, at depths of 1 cm (□), 2 cm (0), 5 cm (Δ),
10 cm (+) in the seed longevity experiment (here 10⁰ = 0).
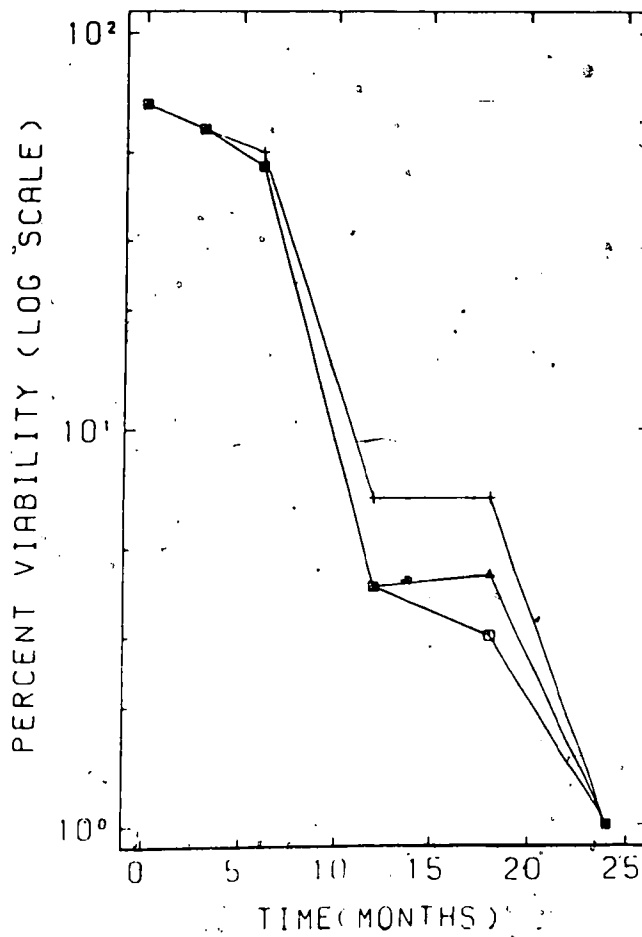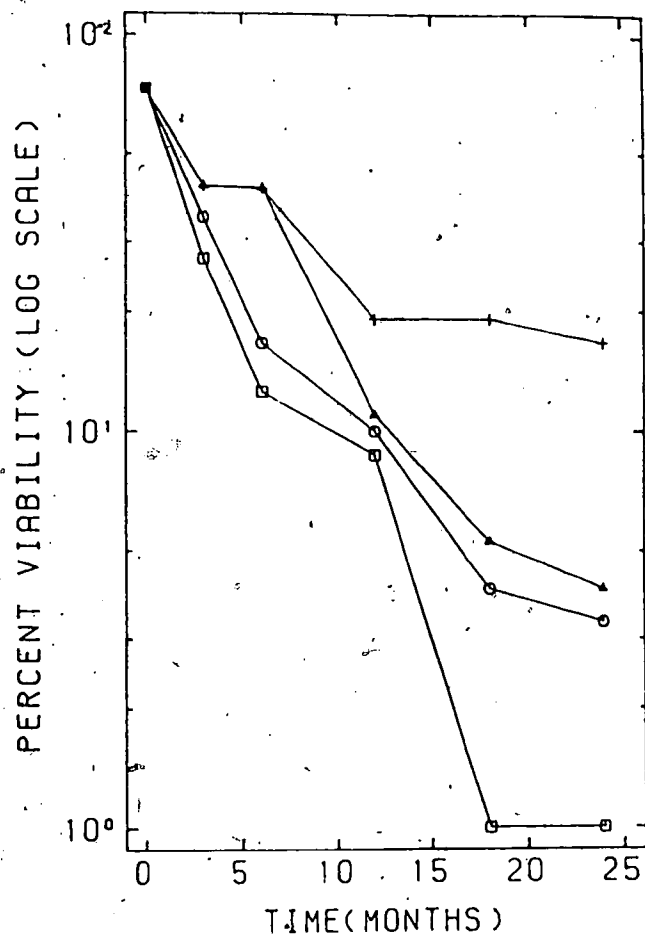
FIG. 3.13 b. Number of viable seeds of A. longifolia (top)
and B. integrifolia (bottom), expressed as a %
of the total, at depths of 1 cm (□), 2 cm (O), 5 cm (Δ),
10 cm (+) in the seed longevity experiment (here $10^0 = 0$).

Table 3.11 Summary of analysis of numbers of viable, dormant seeds
present after 3 to 24 months field storage

Hypothesis tested	G-value				
	3 mths	6 mths	12 mths	18 mths	24 mths
Species x viability independence					
C. monilifera ssp.mon. > ssp. rotundata	3.9**	8.3**	11.0**	5.7**	10.0**
A. longifolia > ssp. rotundata	0.1	1.3	9.6**	4.2**	4.6**
A. longifolia > B. integrifolia	-0.1	-1.1	6.0**	1.5	7.1**
Depth x viability independence					
2 cm > 1 cm	0.2	1.7	0.4	0.5	0.4
5 cm > 1 cm	3.1**	3.7**	2.6*	0.4	0.2
10 cm > 1 cm	2.6*	3.6**	2.3*	4.5**	12.2**

* $P \leq 0.05$ ** $P \leq 0.01$

These three characteristics make a relatively long seed life desirable - a large seed pool is advantageous in the absence of resprouting; seeds may have to survive long periods between fires; and survive at least 12 months between seed inputs.

On the other hand, those with the lowest seed longevity (C. monilifera ssp. rotundata and B. integrifolia) also have common ecological characteristics:

1. The adults resprout after fire and so are not entirely dependent on seed for regeneration after fire.

2. Fire is not necessary for seed germination and, in the case of C. monilifera · ssp. rotundata, appears to reduce it by causing death of seeds at shallow soil depths.

3. Both have an extended flowering season and some seed drop occurs in all months of the year.

These characteristics permit a comparatively short seed longevity - a large seed pool is not necessary after fire except after high intensity fires which may kill adult plants; seeds do not have to remain viable until their germination is induced by fire; and short periods between seed falls means replenishment of old by fresh seed.

Since the soil seed pool is normally more or less continually replenished by fresh seed of C. monilifera ssp. rotundata, its seed longevity would be of practical importance only if such replenishment was prevented.

3.6 Summary

C. monilifera ssp. rotundata has a number of advantages in the seed stage which contribute to its success in Australia. These are:

1. high level of year-round seed production, relatively unaffected by dry conditions;

2. lower overall levels of seed predation compared to A. longifolia and caused mainly by birds while seeds are still on the parent plant (a mean yearly predation of 35%), although predation can

be higher at certain times of the year or if seeds are in clumps on the ground (20% of predated seed was, however, dispersed undamaged);

3. high numbers of seeds in the buried seed pool, resulting from 1 and 2 (although the rate of burial is low, 0.6% per day, loss of single seeds on the ground, 0.9% per day, is also low);

4. comparatively short longevity of buried seed (2% averaged over various soil depths after 2 years), which, although a disadvantage, is offset by the corresponding figure for deeply buried seed (10 cm) of 8%.

By contrast, A. longifolia has:

1. a comparatively low level of seed production which appears to be reduced under dry conditions;

2. high overall levels of seed predation, caused by a variety of predators;

3. low but comparatively constant numbers of viable seeds in the buried seed pool;

4. higher longevity of buried seed than C. monilifera (6% averaged over various soil depths after 2 years, increasing to 20% at a depth of 10 cm).

It is apparent from Table 3.12 that C. monilifera has advantages over A. longifolia, at least up to the seed stage, in all aspects except seed longevity.

A model of seed (and seedling) dynamics can be prepared (Fig. 3.14). In the case of C. monilifera,

$$S_{t+1} = S_t + p - h S_t - b S_t$$
$$= p + S_t(1 - h - b)$$

where p is seed production per plant,
S number of seeds on the soil surface at a certain time (t),
h the fraction predated or lost, and

b the fraction buried.

Values of these parameters for each month may be obtained from sections 3.1 and 3.2.

$$Bl_{t+1} = Bl_t - l_1 Bl_t - g_1 Bl_t + xb S_t$$
$$= Bl_t (1 - l_1 - g_1) + xb S_t$$

and

$$B2_{t+1} = B2_t (1 - l_2 - g_2) + yb S_t$$

where B is the number of seeds buried at depths of 0-2, 2-4 cm,

l the fraction lost,

g the fraction germinated at each depth, and

x and y the proportions of buried seed at depths of

0-2 and 2-4 cm respectively.

From section 3.3,

$x = 0.87$

$y = 0.13$

$b = 0.29$

The values for g may be estimated from later results (Chapter 4), but values for l have not yet been obtained.

$$G = g_0 S_t + g_1 Bl_t + g_2 B2_t$$

where G is the total number of germinants.

G may also be estimated from figures in Chapter 5.

The following chapters were prompted partly by the need for values for some of the above parameters to complete the population' dynamics model of C. monilifera at least to an early growth stage.

MATURE
PLANT

p

Harvesting
+ losses

h

SOIL
SURFACE
(S)

b

Lost

$l_{1,2..}$

BURIED
IN SOIL
(B1,B2..)

g_o

$g_{1,2..}$

GERMINANTS
(G)

JUVENILES
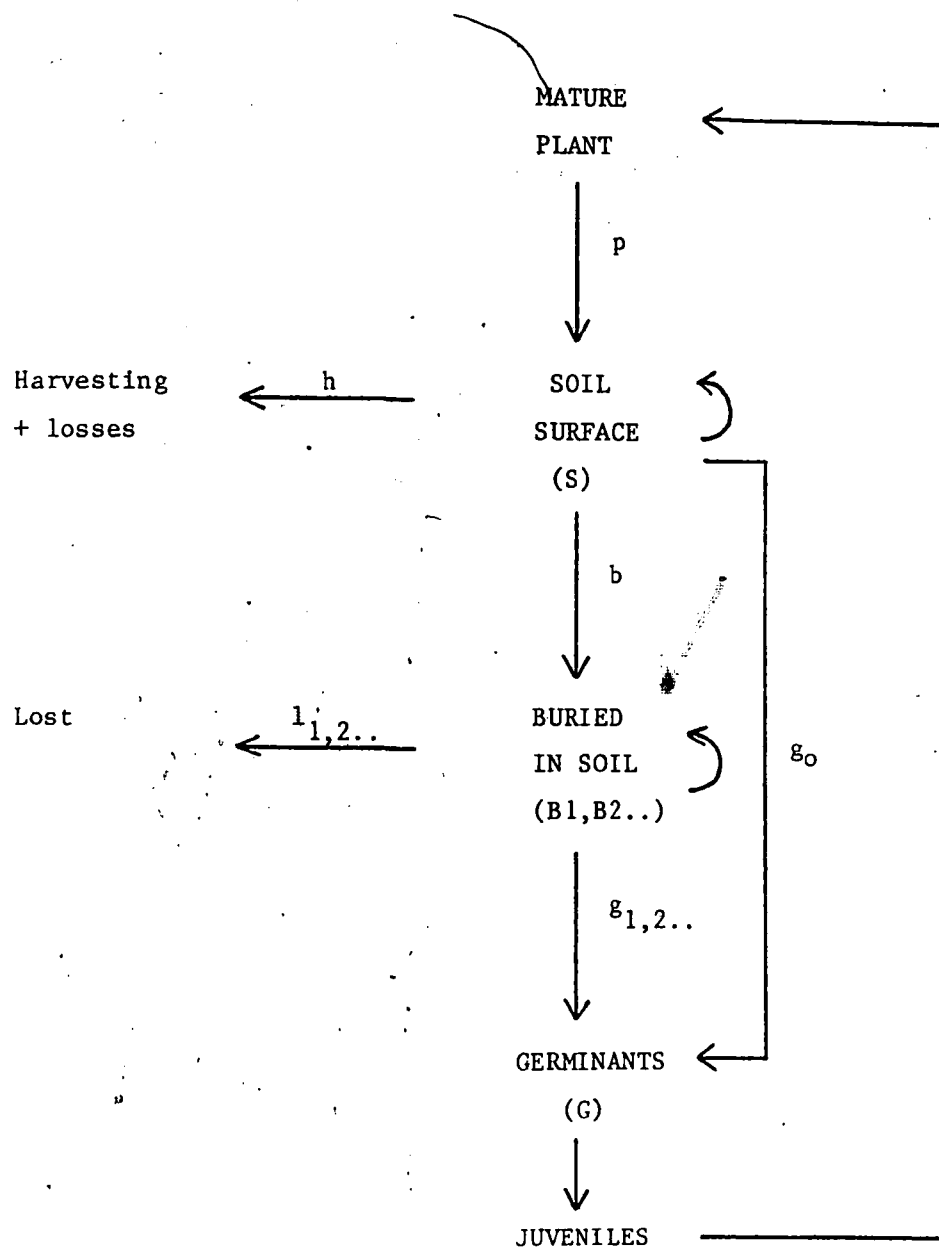
FIG. 3.14. Model of seed and seedling population dynamics
of C. monilifera.

Table 3.12　Summary of seed characteristics of C. monilifera ssp.
　　　　　　　rotundata and A. longifolia in Australia (the higher
　　　　　　　the level, the larger the number of +'s)

	C. monilifera	A. longifolia
Flowering	+++	++
Viable seed production	+++	+
Seed predation	++	+++
Soil seed pool	+++	+
Seed longevity	++	+++

Chapter 4

Germination of
Chrysanthemoides and Acacia

"There is no doubt that the period between successful seed set and seedling establishment is the most precarious in the life cycle of angiosperms."
(Osmond, Bjorkman & Anderson 1980)

"Acacia seed is produced early in the life cycle of a wattle tree and, as its germination is largely dependent on fire, prolific seedling growth is likely to follow a hot bushfire."
(Luke & McArthur 1978)

Introduction

    Once a seed bank is present in the soil, germination of those
seeds is the next stage in the continuation of the population.
Germination is a further important sieve (Harper 1977) through which
considerable losses are likely to occur. This is reflected in the
small number of seedlings usually present compared with the numbers
of seeds in the seed bank. Several workers have found only 1-4% of
weed seed banks present as seedlings (Barralis 1965; Chancellor
1965; Naylor 1972).

    Seed germination may be influenced by various factors including:

1. State of the seed-bed, such as amount of litter and nutrients.
    The previous occurrence of fire can markedly affect the physical
    and chemical composition of the seed-bed.

2. Fire which can result in breaking dormancy of seeds or in their
    death or in altering the state of the seed-bed.

3. Temperature – certain temperature regimes may be necessary to
    break dormancy but temperature extremes may prevent germination.

4. Osmotic potential of the soil solution – usually more
    germination occurs at higher potentials.

    I investigated each of these factors, particularly on seeds of
C. monilifera ssp. rotundata and A. longifolia, in a field experiment
in the case of 1 above, in three field experiments in the case of 2
and in the laboratory in the case of 3 and 4. I extrapolated from the
laboratory experiments to the behaviour of C. monilifera and
A. longifolia in the field.

4.1 Seed bed

4.1.1 Introduction

The state of the seed-bed may be important for germination and/or establishment of the study species since most C. monilifera seedlings are present in the litter underneath the parent plants. This may be due also to most of the seeds remaining under parent plants (Chapter 3). However, litter may shield seeds and seedlings from temperature or moisture stress and protect them from predators (Shaw 1968 a, b; Griffin 1971).

Fire is also likely to affect the seed-bed in various ways besides having direct effects on germination.   Thus the previous occurrence of fire may increase the numbers of seedlings establishing, owing to sterilisation of microbial populations which occurs in intense fires and which results in a prolonged process of recolonisation (Renbuss, Chilvers & Pryor 1972). Such sterilisation may reduce the incidence of pathogenic fungi such as Fusarium sp.

Changes in soil nutrient levels from nutrient release from ash (Specht, Rayson & Jackman 1958; Siddiqi, Carolin & Myerscough 1976) and from breakdown of microbial thalli (Pryor 1960) are known.   This usually leads to enhanced growth rate of seedlings and may result in increased numbers establishing if they reach a critical size before the advent of adverse conditions such as temperature or moisture stress.

In the present study, I investigated the effects of various seed-beds on seedling emergence and establishment by sowing seeds of a range of species in burnt and unburnt areas and superimposing litter and nutrient treatments in the latter.

4.1.2 Methods

An experiment was conducted during 1981 to determine the effect of various seed-beds, particularly on C. monilifera ssp. rotundata and A. longifolia. C. monilifera ssp. monilifera was also used since it can also occur in a coastal habitat. A. cyclops was included since it occurs in similar habitats in Western Australia.

Treatments were:

(a) Control

(b) Litter removed

(c) Litter removed, nutrients added

(d) Previously burnt

Nutrients were applied in pelleted form immediately after sowing in March 1981 as a complete fertiliser ("Osmocote") at the rate of 1670 kg/ha which contained 250 kg/ha of nitrogen. Treatment (d) was provided by a wild-fire in November 1980, with the other treatments located c. 50 m away. There were eight replications, with 75 seeds of each species per replication sown 1 cm deep.

Plots were c. 1 m away from mature plants but shaded for most of the day. Seedlings were counted and marked with toothpicks 4, 7, 10, 13, and 16 weeks after sowing.

Numbers of seedlings were calculated as percentages of the number of sown seeds and were arcsine transformed before ANOVA analysis. (Sokal & Rohlf 1969, p. 386). Untransformed numbers are given in the results.

4.1.3 Results

Burnt areas provided the best seed-bed conditions for both sub-species of C. monilifera and A. cyclops in terms of seedling numbers (Table 4.1). There was comparatively poor emergence of A. longifolia in all treatments. Some frosts occurred after the final counts which appeared to markedly affect the survival of C. monilifera ssp. rotundata but not ssp. monilifera.

4.1.4 Discussion

When seeds were sown after fire, better seed-bed conditions were provided for both sub-species of C. monilifera and A. cyclops than in unburnt areas. Emergence of A. longifolia appeared to be independent of seed-bed conditions, but if seeds are present in the soil before a fire, germination and emergence can be markedly stimulated (see section 4.2).

Numbers of seedlings of C. monilifera ssp. rotundata were higher in plots with the litter removed than that observed in other experiments (eg. Chapter 7) when seeds were sown in the open with little litter present. This may have been due to the plots in the present experiment being somewhat sheltered whereas there is likely to

Table 4. 1 Mean number of seedlings per plot in various seed bed treatments from 75 sown seeds. Standard errors are in parentheses

Treatment	Species	Time after sowing (weeks)					Total
		4	7	10	13	16	
Control	C. mon. ssp. mon.	33.9(4.0)	37.0(3.6)	20.6(6.2)	23.6(9.6)	19.8(7.0)	40.5
	C. mon. ssp. rot.	3.0(1.7)	6.0(1.7)	6.0(3.0)	6.9(2.6)	12.9(2.6)	13.2
	A. longifolia	0	1.0(1.0)	0	0	8.9(6.0)	8.9
	A. cyclops	0	0	2.0(1.0)	2.8(1.7)	1.0(1.0)	2.8
No litter	C. mon. ssp. mon.	25.8(9.5)	26.7(8.7)	26.3(8.7)	26.7(9.6)	30.0(9.2)	31.0
	C. mon. ssp. rot.	1.0(1.0)	9.2(6.0)	17.1(7.0)	21.2(6.2)	25.8(7.2)	25.8
	A. longifolia	0	0	0	0	1.0(1.0)	1.0
	A. cyclops	0	0	0	0	4.0(2.0)	4.0
No litter	C. mon. ssp. mon.	8.1(4.4)	17.8(6.2)	7.1(1.0)	7.2(3.6)	8.9(4.6)	20.6
+ nutrients	C. mon. ssp. rot.	4.0(1.0)	6.0(3.0)	6.9(4.0)	12.1(9.0)	12.1(9.0)	12.1
	A. longifolia	0	0	0	0	6.0(3.0)	6.0
	A. cyclops	0	0	1.0(1.0)	1.0(1.0)	10.1(6.1)	10.1
Burnt	C. mon. ssp. mon.	44.9(1.7)	45.8(2.6)	47.1(2.0)	47.1(2.0)	47.1(2.0)	47.1
	C. mon. ssp. rot.	22.0(2.0)	28.1(2.0)	28.1(2.0)	32.2(2.0)	33.2(3.0)	33.2
	A. longifolia	0	0	1.0(1.0)	2.0(1.0)	5.2(1.0)	5.2
	A. cyclops	3.1(1.7)	6.0(3.0)	5.1(3.6)	9.0(3.0)	14.1(2.0)	15.0

have been greater moisture and temperature stress in more exposed situations in the other experiments.

4.2 Fire

4.2.1 Introduction

Numerous studies have emphasised the importance of the alteration in the seed-bed following fire in increasing seed germination of a wide range of species. (Beadle 1940, Cremer & Mount 1965, Floyd 1976, Purdie 1976, 1977). Germination effects may be limited to those seeds comparatively close to the soil surface since surface soil temperatures during a fire may be $>200°C$ but temperatures $>100°C$ rarely occur below 5 cm (Beadle 1940).

One reason for increased germination is the effect of heat in breaking dormancy of "hard" seeds. For example, the germination of A. longifolia var. sophorae was increased from 14% to 32% by heating the seed at 105°C for 10 min (Aveyard 1968). Germination of C. monilifera ssp. monilifera was markedly increased after exposing seeds within weathered pericarps to 100°C for 30 s (Lane & Shaw 1978). Such temperatures are usual in a fire of low intensity but seeds of many native species such as Acacia are unlikely to germinate following such a fire, with increasing numbers establishing as the intensity of the fire increases (Christensen & Kimber 1975).

I investigated the effect both of low and high intensity fires on emergence of previously sown C. monilifera ssp. rotundata and A. longifolia to determine if the imbalance in density of seedlings of the two species in the study area could be redressed more in favour of the native species.

4.2.2 Methods

Three experiments were conducted at Moruya in 1980 and 1981 (Table 4.2). Extra fuel in the form of small branches were placed on the plots burnt in the "high intensity fire" experiments.

Maximum temperatures during the fires were estimated by marking the unglazed surface of tiles with "Thermochrom" crayons and placing these on the soil surface, crayon surface upwards, after wrapping in alfoil.

Table 4.2   Summary of fire experiments at Moruya

Experiment	Date of burning	Date of sowing	Timing of counts after sowing	Species sown	No. seeds /rep.	Depth of sowing (cm)	Repli-cations
"Low intensity fire"	March 1980 (1 week after sowing)	March 1980	1-5 months	C.mon. ssp. rot. A. longifolia	100	0, 0.1, 1, 5	8
"High intensity March fire"	March 1981 (1 week after sowing)	March 1981	1-4 months	C.mon. ssp. rot. A. longifolia (treated)	100	0, 0.1, 1, 5	8
"High intensity August fire"	August 1981 (1 week after sowing)	August 1981	1-4 months	C.mon. ssp. rot. A. longifolia	100	0.1, 1, 5	8

Table 4.3 Mean number of seedlings of C. monilifera and
A. longifolia in plots burnt or unburnt 5 months after
sowing in the "low intensity fire" experiment. Standard
errors are in parentheses

| Depth of sowing | C. monilifera | | A. longifolia | |
cm	Control	Burnt	Control	Burnt
0	0	0	0	0
0.1	0	0.3 (0.3)	0	0
1.0	0.3 (0.3)	1.3 (0.3)	1.7 (0.3)	0
5.0	0.3 (0.3)	0.3 (0.3)	0	8.3 (2.0)

Table 4.4 Mean number of seedlings of C. monilifera and A. longifolia in plots burnt or unburnt 4 months after sowing in the "high intensity March fire" experiment. Standard errors are in parentheses

Depth of sowing cm	C. monilifera		A. longifolia	
	Control	Burnt	Control	Burnt
0	3.7 (1.3)	0	0	0
0.1	28.0 (5.4)	0	4.0 (1.8)	0
1.0	21.2 (7.1)	0	5.2 (1.1)	6.0 (2.2)
5.0	16.2 (6.8)	9.0 (1.9)	18.0 (3.8)	14.0 (3.6)

Table 4.5 Mean number of seedlings of C. monilifera and A. longifolia in plots burnt or unburnt 4 months after sowing in the "high intensity August fire" experiment. Standard errors are in parentheses

Depth of sowing cm	C. monilifera		A. longifolia	
	Control	Burnt	Control	Burnt
0.1	1.5 (0.6)	0	0	0
1.0	9.5 (4.3)	0.5 (0.3)	0	8.0 (2.7)
5.0	13.5 (3.9)	4.25 (2.2)	1.25 (0.7)	10.0 (3.8)

Seeds were untreated except in the "high intensity March fire" experiment where A. longifolia seeds were immersed in boiling water before sowing.

Numbers of seedlings were calculated as percentages of the number of sown seeds and arcsine transformed before ANOVA analysis (Sokal & Rohlf, 1969). Untransformed numbers are given in the results.

4.2.3 Results
"Low intensity fire" experiment

Maximum surface temperatures during burning varied from 100°C to 300°C. Rainfall in the 4 months after sowing was low (95 mm). Seedling emergence was generally poor (Table 4.3) but there were significantly more seedlings of A. longifolia in the burnt plots than seedlings of either species in the other treatments (ANOVA, $P \leq 0.05$).

"High intensity March fire" experiment

Maximum surface temperatures during burning varied from 500°C to 600°C. Rainfall in the 4 months after sowing amounted to 251 mm. No emergence of C. monilifera occurred in burnt plots from seeds sown from 0 to 1.0 cm or of A. longifolia from 0 to 0.1 cm (Table 4.4). The number of seedlings of C. monilifera in the unburnt plots was significantly greater than numbers in the other treatments (ANOVA, $P \leq 0.05$).

"High intensity August fire" experiment

Maximum surface temperatures during burning varied from 500°C to 600°C. Rainfall in the 4 months after sowing amounted to 249 mm. No emergence of either species occurred in burnt plots from seeds sown at 0.1 cm and little of C. monilifera at 1.0 cm (Table 4.5). The numbers of C. monilifera in the unburnt plots and of A. longifolia in the burnt plots were significantly greater than numbers in the other treatments (ANOVA, $P \leq 0.05$). Significantly more seedlings emerged from 5.0 cm than 0.1 cm.

4.2.4 Discussion

Emergence from untreated seeds of A. longifolia was stimulated by fire but in burnt plots there was no emergence of A. longifolia in any experiment from seeds at 0 or 0.1 cm. These may have either been killed by fire or predated (Chapter 3). Soil moisture is also likely

to have been less near the soil surface since most emergence came from seeds at a depth of 5 cm.

Predation is less likely to have affected seeds of *C. monilifera* (Chapter 3) and so the poor emergence from seeds down to at least 1 cm in burnt plots appears to be largely due to fire killing these seeds. Soil moisture may also have contributed to limiting emergence from seeds nearer the soil surface. In unburnt plots a satisfactory level of emergence of *C. monilifera* came from seeds >0.1 cm deep in the "high intensity March fire" experiment and >1 cm deep in the "high intensity August fire" experiment.

I conclude that the use of fire is likely to be a useful control measure for buried seed of *C. monilifera* ssp. *rotundata* especially since most viable seeds in the seed bank are buried at a soil depth of 0 - 2 cm (Chapter 3). Accordingly, further experiments using fire in a program of controlled burning were conducted (Chapter 10).

4.3 Temperature

4.3.1 Introduction

In his review of seed germination, Johnston (1979) has pointed out the ecological importance of temperature. Temperature of the seed-bed can vary both seasonally and diurnally, the extent depending on factors such as aspect, amount of litter, soil moisture, plant cover and depth in the soil profile.

Different seeds have different temperature ranges within which they germinate. Thus the wider the range, the more likely will a greater proportion of the soil seed pool germinate before it is lost through predation, disease or decay. There is usually an optimal temperature, at which the highest percentage of germination is attained in the shortest time (Mayer & Poljakoff-Mayber 1963). It would be expected that when the majority of seeds experience such an optimum, provided other conditions such as dormancy or moisture are not limiting, a "flush" of germination would occur.

In the case of *C. monilifera* ssp. *rotundata*, Aveyard (1971) found the highest percentage germination to be at 25°C when counted at 21 days. Expression of such a final figure, however, reveals nothing about the rate of germination. Some measure of this can be obtained by plotting the cumulative number of germinated seeds against time (Roberts 1972). Alternatively, germination character curves, which

show for each day after sowing the maximum and minimum temperatures. at which there is 50% germination of the final maximum, can be prepared (Thompson 1973a). The relationship between temperature and rate of germination can also be used to compare different seed lots by plotting temperature against the rate (expressed as the reciprocal of the number of days) of 50% germination of the final maximum (Hegarty 1973).

I incorporated these various measures by investigating the germination of both sub-species of C. monilifera and A. longifolia at a range of temperatures experienced in the soil and provided in the laboratory by a thermo-gradient plate.

4.3.2 Methods

A thermo-gradient plate similar to that described by Thompson (1970a) and Fox & Thompson (1971) was used. After stabilisation for 3 days, thermocouples, connected to a continuous recorder, were placed at three permanent positions on the plate. Weathered seeds of both sub-species of C. monilifera and of A. longifolia cut at the distal end were used. They were placed on germination paper moistened with distilled water and 0.05% benomyl fungicide in rows corresponding to 11 temperatures ranging from $9.5 \pm 0.7°C$ to $34.5 \pm 0.8°C$. Successive temperatures varied from one another by $1.0°C$ to $3.5°C$. All temperatures were checked twice each week with a temperature probe attached to a multimeter. There were three replications of 25 seeds of each species. Observations were made at 1 to 3 day intervals for 7 weeks after the seeds were placed on the plate. Seeds were kept on the plate for 5 days after germination and the length of their radicle then measured to check on temperature effects on early growth of the radicle.

4.3.3 Results

Germination commenced 2 days after sowing C. monilifera ssp. monilifera and after 3 days with the other species (Fig. 4.1). The optimum temperature for all species in terms of rate of germination to 50% of the maximum was between 21°C and 25°C (Fig. 4.2). All species germinated to at least this degree (50%) over a comparatively wide range of temperatures, with that of C. monilifera ssp. monilifera extending c. 3°C higher than the others (Fig. 4.2). At low temperatures (13°C and 16°C), rate of germination of both sub-species of C. monilifera was significantly greater than that of A. longifolia (ANOVA, $P \leq 0.05$) (Fig. 4.3). Radicle elongation in
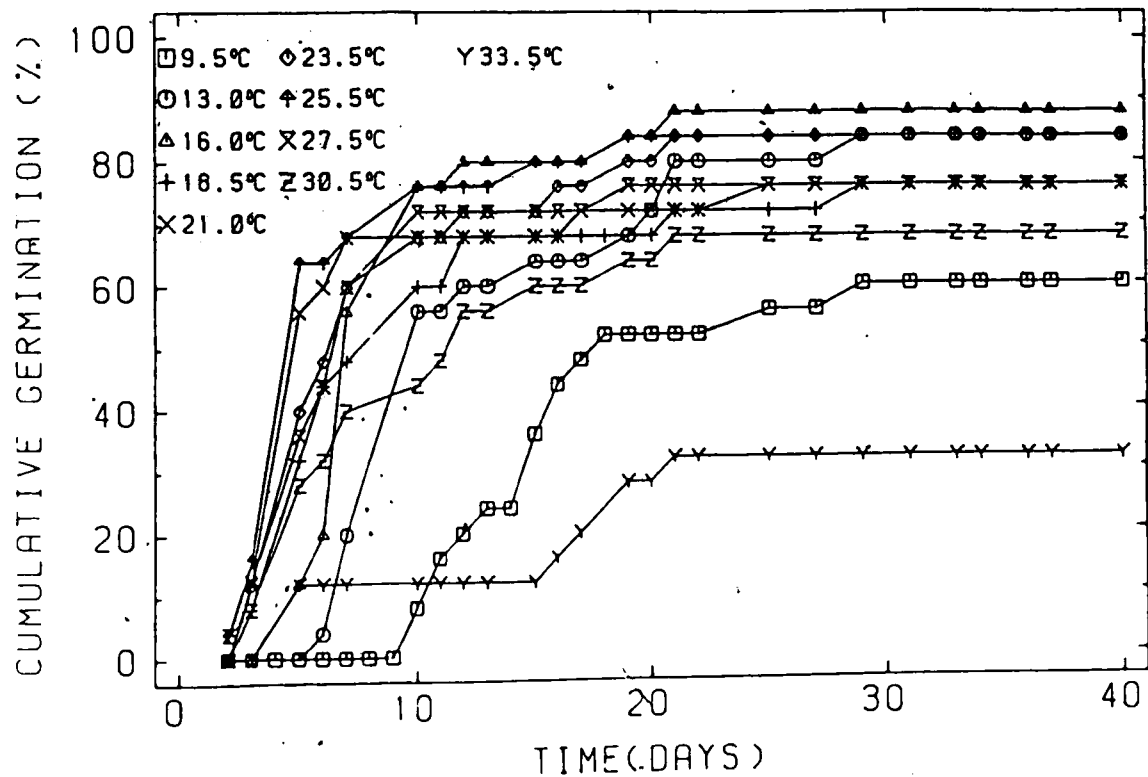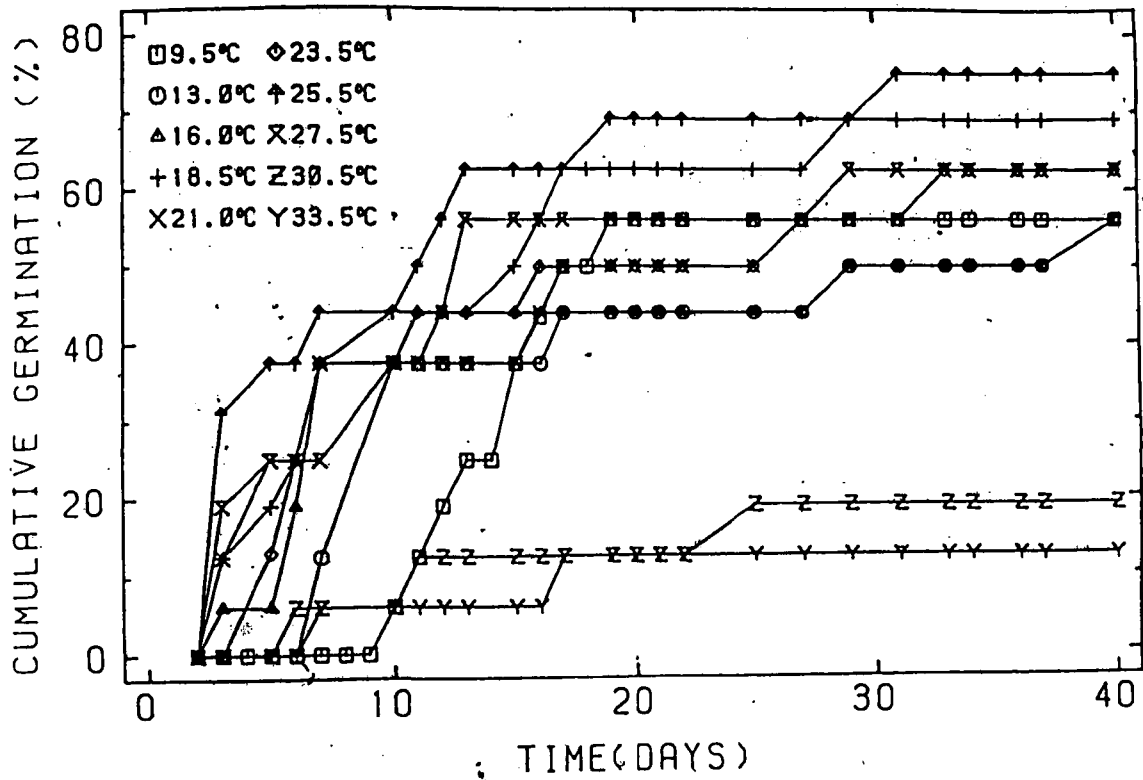
FIG. 4.1 a. Cumulative germination, expressed as a percentage of the total number of seeds, of C. monilifera ssp. rotundata (top) and C. monilifera ssp. monilifera (bottom) at 10 temperatures.

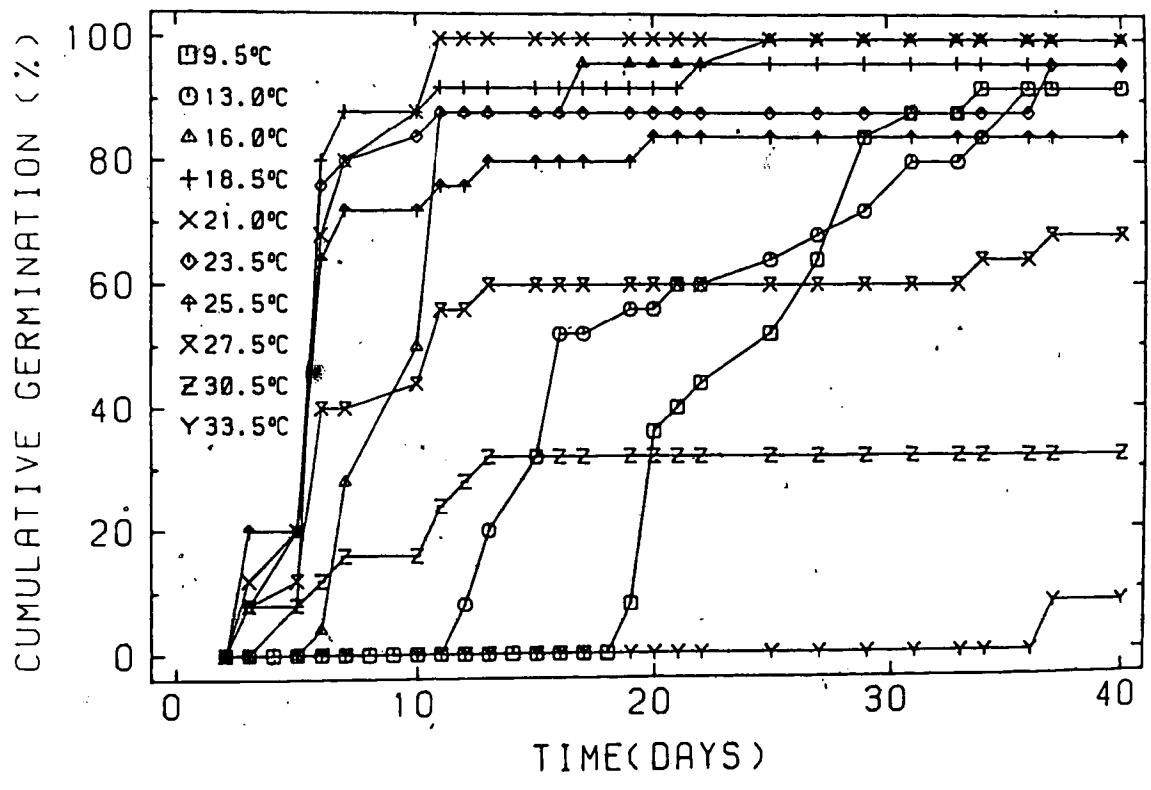FIG. 4.1 b. Cumulative germination, expressed as a percentage of the total number of seeds, of A. longifolia at 10 temperatures.
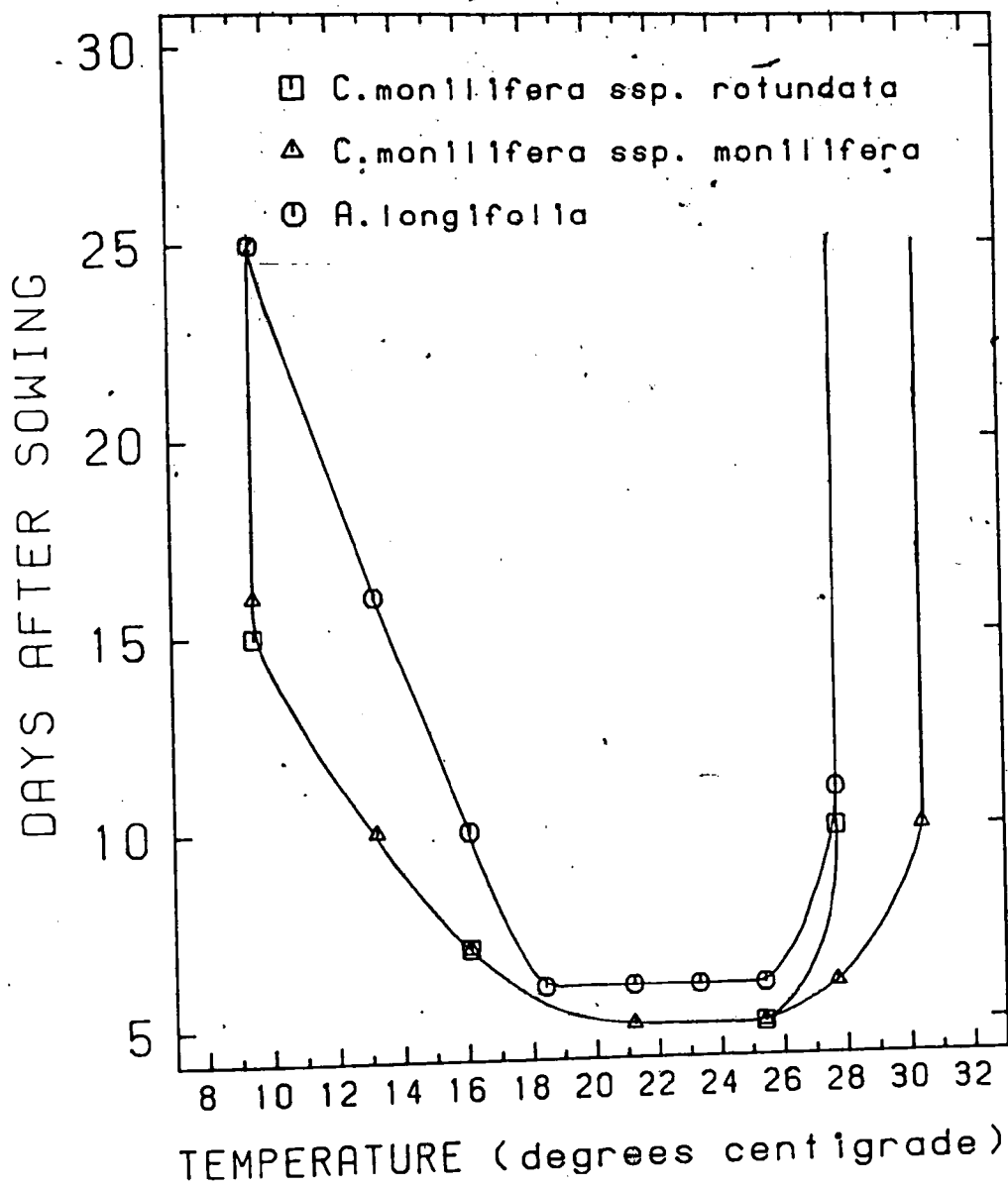
FIG. 4. 2.   Number of days to 50% of the maximum germination of
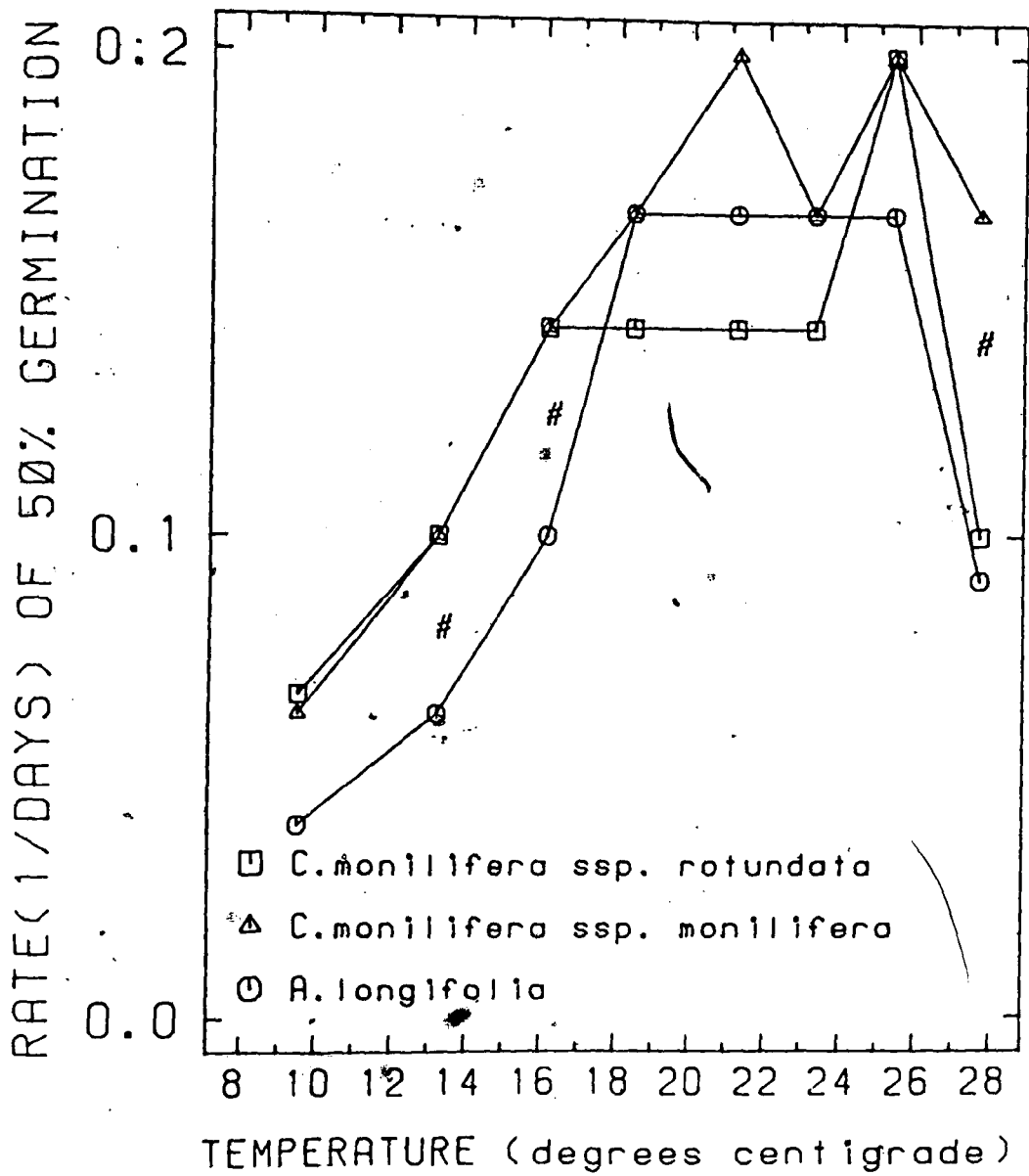C. monilifera and A. longifolia at a range of
temperatures.

FIG. 4.3.   Rate of germination, expressed as the reciprocal of the number of days to 50% germination, of C. monilifera and A. longifolia. Significant differences (P < 0.05) are shown by #.

each case was greatest between 21°C and 25°C, with some necrosis of radicles at higher temperatures.

4.3.4 Discussion

The wide range of germination temperatures of the species investigated indicates their potential to germinate at most times of the year. In fact, seedlings of C. monilifera ssp. rotundata emerged in the field every month except November and December (Chapter 5). The wider temperature range of C. monilifera ssp. monilifera may thus enable it to germinate at any time of the year and in a wide range of habitats, but no field data are available to substantiate this. Most emergence, however, has been observed in autumn (Parsons 1973).

Where seeds of both C. monilifera ssp. rotundata and A. longifolia are present in the field, the faster germination rate of the former at low temperatures would be to its advantage in competition with A. longifolia, since even a few days precocity in germination and emergence time can have major effects on subsequent vigour (Ross & Harper 1972; Weiss 1981a).

4.4 Osmotic potential

4.4.1 Introduction

Soil moisture potential has two components: osmotic potential of the soil solution and matric potential at which soil water is held on the substrate. These were equivalent in their effect on the germination of dehulled seeds of Phalaris tuberosa (phalaris) but with intact seeds, the seed coat provided a large resistance to the absorption of soil water and their equivalence no longer held (McWilliam & Phillips 1971). In the latter case, the results of germination under osmotic stress must be used with caution in predicting the germination behaviour of seeds in dry soil. Soil conductivity and soil/seed contact phenomena also become important in the field (Army & Hudspeth 1960).

Osmotic potential has been used often, nevertheless, to compare drought resistance in germination of different species (Hunter & Erickson 1952; McGinnies 1960; Parmar & Moore 1966). Increasing the osmotic potential either delays germination or reduces the rate and total germination. Osmotic agents such as mannitol (Wiggans & Gardner 1959) and polyethylene glycol (Jackson 1962) have been used because of their relative stability and inertness, high molecular weight,

solubility in water and non-toxicity even at high concentrations.

I decided in the present study to compare the effect of osmotic potential on germination both of intact seeds of C. monilifera ssp. rotundata and of A. longifolia and those in which the seed coat or pericarp had been removed or treated to allow ready absorption of water. Some treatment, such as seed weathering or fire, is necessary for satisfactory germination of A. longifolia and treatment of C. monilifera is indicated by the poor germination of freshly harvested seed (Aveyard 1971). I decided also to compare the germination of the two species in the above experiment with that in dry soil.

4.4.2 Methods

Seeds of C. monilifera ssp. rotundata (harvested 6 weeks before use) and A. longifolia were used to compare germination over a range of osmotic potentials. Seeds of A. longifolia were nicked at the distal end with a scalpel before use. Either intact seeds of C. monilifera ssp. rotundata or those in which the pericarp had been split open and removed, leaving only the embryo and endosperm, were also tested (Fig. 4.4).

The seeds were first exposed to an osmotic potential of -0.5 MPa by placing them in petri dishes on filter paper saturated with aqueous solutions of either mannitol or polyethylene glycol. The depth of the solution was c. 1mm and the dishes were sealed to prevent evaporation. There were no significant differences in either species between the results with mannitol or polyethylene glycol (t-test, $P > 0.05$), so that in future only mannitol was used, to give potentials of 0, -0.5, -0.75, -1.0, -1.5 MPa. There were 4 replications of 25 seeds each, kept in a germination cabinet at $20\pm1°C$ and with a 12 h photoperiod.

Germination was recorded over a period of 36 days. Ungerminated seeds were then removed and tested for germination in water as above to check that mannitol had only reduced the availability of water and had not entered the seed.

In order to compare water uptake in C. monilifera by the embryo and endosperm with and without the surrounding pericarp, the air-dry weight of each was first obtained and then the weight after 24, 48 or 72 h in water as described above, after removal of excess water in a buchner funnel by vacuum filtration. The pericarp was separated from intact seeds before each weighing.

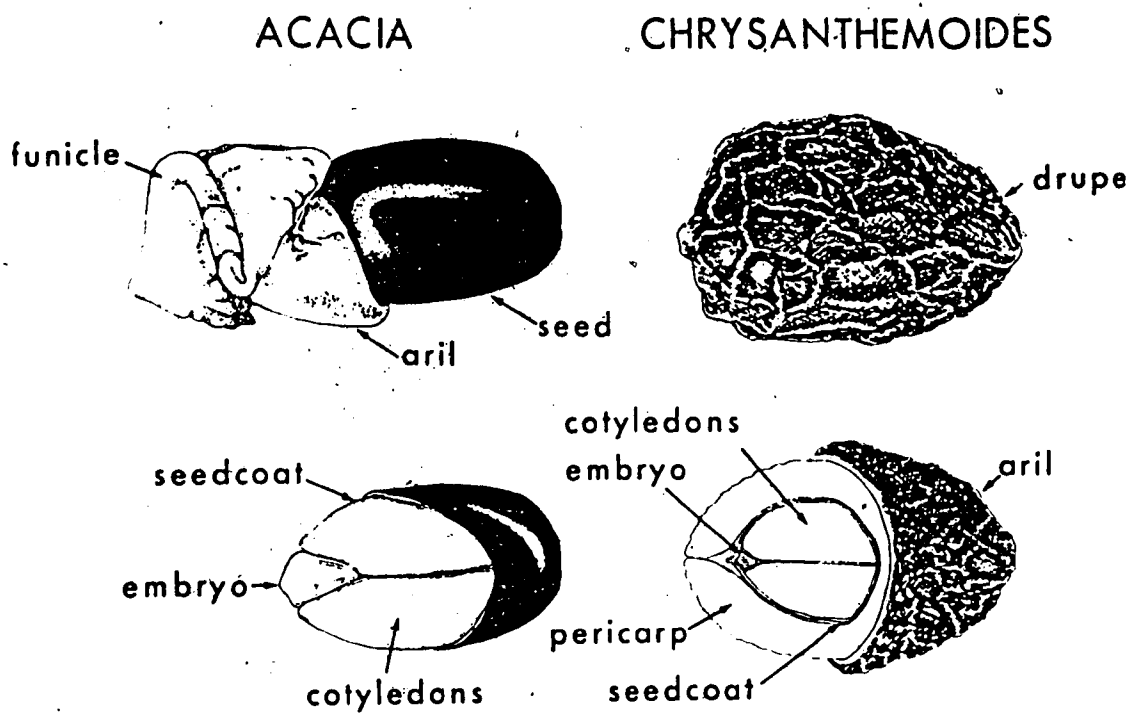## ACACIA CHRYSANTHEMOIDES

FIG. 4.4. Reproductive structures of A. longifolia and
C. monilifera ssp. rotundata. The entire fruit of
A. longifolia is not shown; the funicle is attached
to the pericarp or pod, the fruit being a legume.
Scale is 10:1.

Table 4.6 Weight in mgm of embryo + endosperm and pericarp in intact and opened
seeds of C. monilifera at three times after contact with water.
Percentage increases in weight are shown in parentheses after the
standard errors

Hours after commencement	Intact seeds		Opened seeds	
	Embryo + endosperm	Pericarp	Embryo + endosperm	Pericarp
0	7.6+0.3	26.3+1.2	7.2+0.2	27.3+1.2
24	9.6+0.3 (26.3)	33.9+1.5 (28.9)	9.6+0.3 (33.3)	37.1+2.3 (35.9)
48	9.7+0.3 (27.6)	36.6+1.9 (39.0)	10.0+0.4 (38.9)*	40.3+2.2 (47.6)
72	10.0+0.4 (31.6)	38.0+2.1 (44.5)	– **	41.9+2.0 (53.5)

* germination had commenced (germinated seeds were not weighed)
** 50% of seeds had germinated

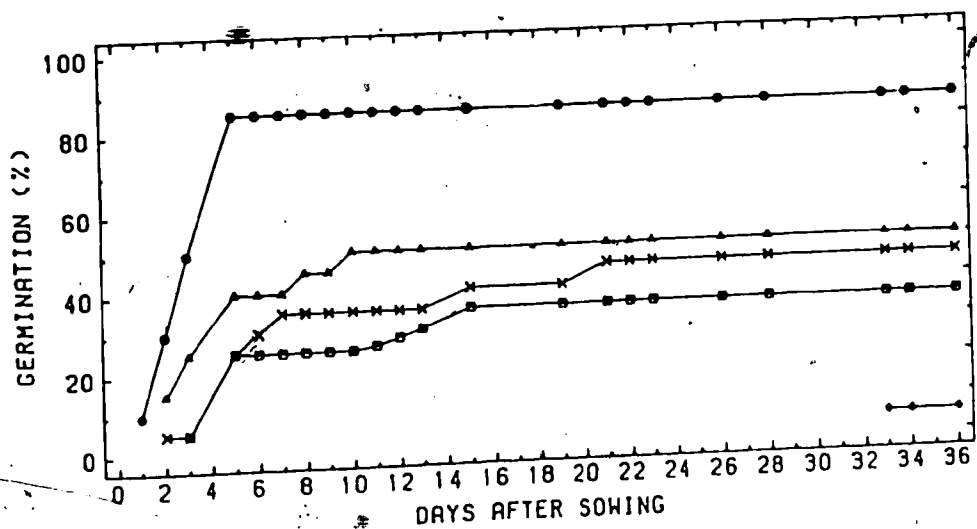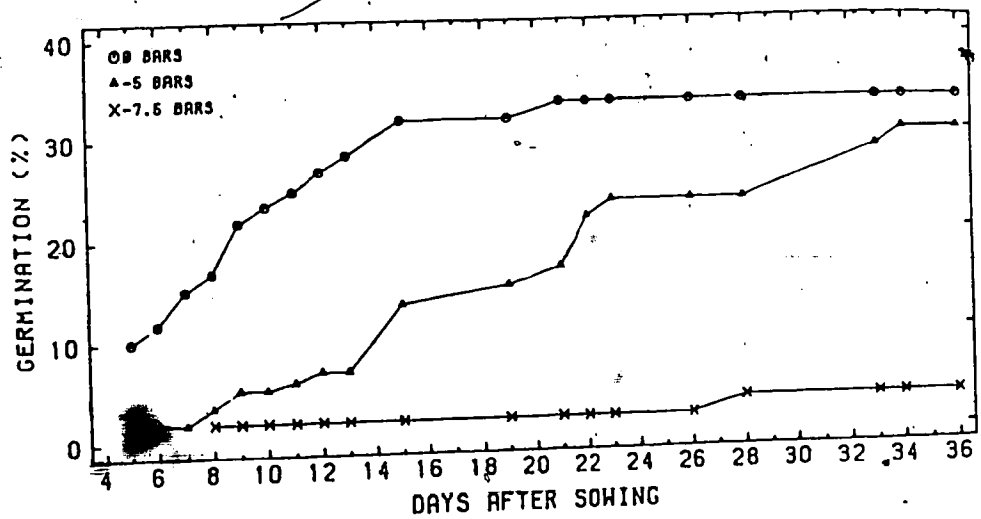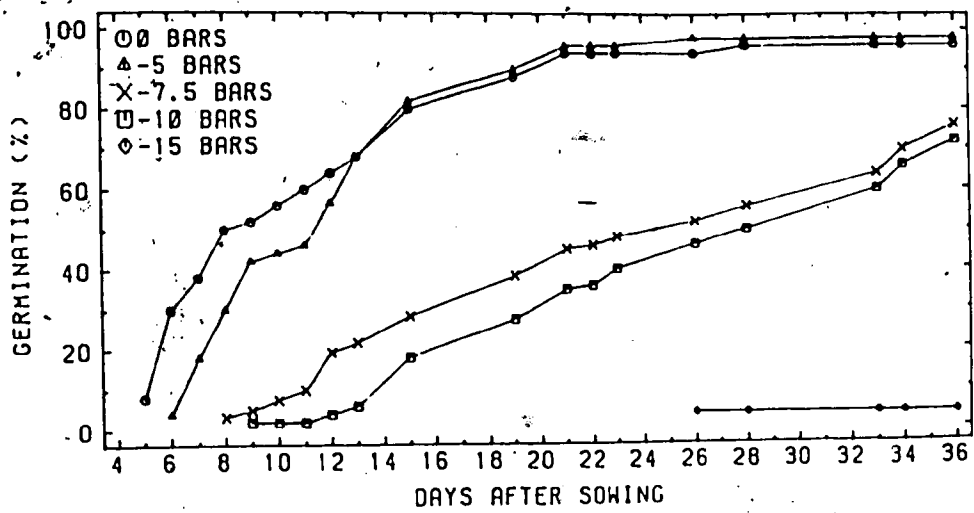FIG. 4.5. Cumulative germination, expressed as a percentage of the total number of seeds, of A. longifolia (top) and intact seeds (middle) and open seeds (bottom) of C. monilifera ssp. rotundata at a range of osmotic potentials (1 MPa ≡ 10 bars).
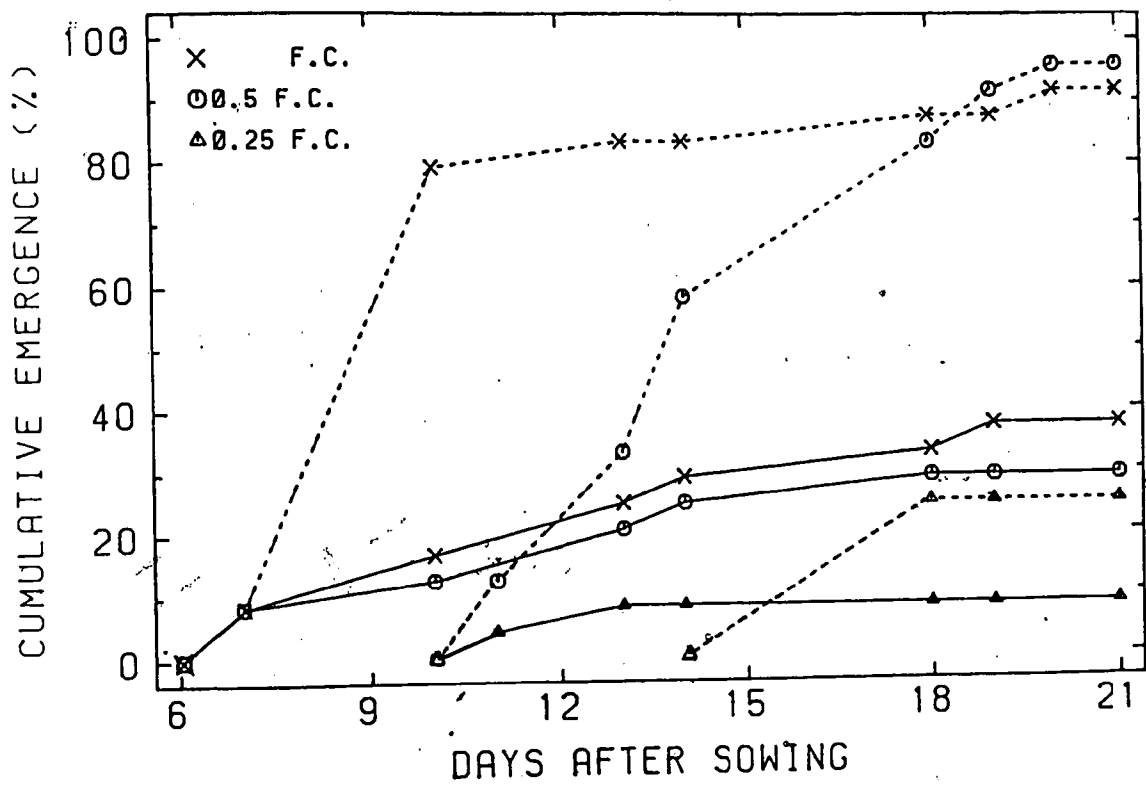
FIG. 4.6.   Cumulative emergence of C. monilifera ssp. rotundata
            (solid lines) and A. longifolia (dashed lines) in
            sand at 25, 50, 100% of field capacity.

Germination in soil was measured with the intact seeds of C. monilifera and cut seeds of A. longifolia used above. These were buried in dune-sand, moistened to 25, 50 or 100% of field capacity, in petri dishes. Emergence was recorded over a period of 3 weeks.

4.4.3 Results

There was a greater uptake of water by the embryo and endosperm of C. monilifera when the pericarp was removed, leading to germination of the opened seeds during the experiment (Table 4.6).

In both species the germination rate and total germination decreased with decreasing osmotic potential, but the pattern of response differed markedly (Fig. 4.5). There were significant differences in germination between intact and opened seeds of C. monilifera at all osmotic potentials (ANOVA, $P \leq 0.01$). In A. longifolia and intact seeds of C. monilifera, there were no significant differences in final germination between 0 and -0.5 MPa or between -0.75 and -1.0 MPa (ANOVA, $P > 0.05$). Mannitol was not absorbed by the seeds since there were no significant differences in germination between seeds taken out of mannitol and controls (ANOVA, $P > 0.05$).

In sand at 25% and 50% of field capacity, emergence of A. longifolia was some days slower than that of C. monilifera although there were no significant differences in final germination of seeds of either species at 50% and 100% of field capacity (ANOVA, $P > 0.05$) (Fig. 4.6).

4.4.4 Discussion

The importance of the seed coat in A. longifolia and the pericarp in C. monilifera ssp. rotundata in germination are obvious. Results of previous tests have shown little or no germination of untreated seeds of A. longifolia. It appears that the embryo and endosperm of C. monilifera ssp. rotundata must imbibe c. 40% of their weight in water before germination can occur. This happens more readily in opened seeds in which both rate and final germination were much greater than in intact seeds. Aveyard (1971) found that intact seeds of C. monilifera ssp. rotundata imbibed 67% of their own weight within 48h.

Weathering of seeds (and subsequent cracking of the pericarp) would be expected to produce similar results to those of the open seeds in this study since heat stimulated germination only of weathered, cracked seeds of ssp. monilifera (Lane & Shaw 1978). In preparation of material for glasshouse work (Chapters 7 and 8), I found that weathering (and subsequent enhancement of germination) could be simulated in ssp. rotundata by successive wetting and drying cycles and heating at 40°C.

The seed coat of A. longifolia has a smooth polished appearance (Fig. 4.4) which makes it difficult to wet in the field. The comparatively small aril may be able to absorb some water but, being at one end of the seed, is easily lost after seed fall and sometimes selectively removed by ants. On the other hand, the pericarp of C. monilifera ssp. rotundata has a ribbed appearance which ensures that it wets readily. It is also covered by the aril which retains moisture for some time after seed fall and which could also take up soil moisture. The aril could thus act as a buffer against drying of the micro-environment around the seed.

Open or treated seeds of both species germinated satisfactorily (although less than at 0 MPa) at comparatively high stress levels (-1.0 MPa). Germination of 74% of A. longifolia at this potential is comparable to the unusually high 80% reported for perennial ryegrass (Lolium perenne) by McWilliam & Phillips (1971). However, there was some days delay in germination of A. longifolia compared to that of open seeds of C. monilifera. Although there was little germination at -1.5 MPa, few seeds germinate at such a potential since it is usually in the vicinity of the permanent wilting point for most plants (Doneen & MacGillivray 1943; Hadas 1970).

Low soil moisture did not prevent emergence of A. longifolia, which was again slower than that of C. monilifera. This delay is likely to give an advantage to the one emerging earlier in a competitive situation between two species (Weiss 1980).

Nevertheless, both species appear adapted to germinate in the usually low soil moisture levels present in the dune sands in this study (Chapter 6), provided there has been some weathering of the seeds.

4.5 Summary

All of the factors investigated had some effect on the germination of C. monilifera and A. longifolia (Table 4.7). C. monilifera, which has already been shown to have a larger seed pool than A. longifolia (Chapter 3), has no serious disadvantages in the germination process. In the field, A. longifolia appears to undergo slower seed weathering and germinates best only after fire. Even though C. monilifera suffers comparatively high seed mortality in a fire, those seeds surviving show higher germination and survival in the seed bed following the fire. The end result is that higher densities of seedlings of C. monilifera than of A. longifolia are usually seen in Australia, whether an invaded area has or has not been burnt. The population dynamics of such seedlings were investigated in the next chapter.

Table 4.7   Summary of factors affecting seed germination of C.   monilifera ssp.
            rotundata and A.   longifolia

	C. monilifera ssp. rotundata	A. longifolia
Fire	Not necessary for germination, shallow seeds killed by hot fires.	Stimulates germination, shallow seeds killed or lost to predators.
Seed bed	Best in a seed bed produced by fire but germinates well under parent plants in unburnt seed beds.	No preference for seed beds.
Temperature	Optimum between 21°C and 25°C. Faster rate than A. longifolia at 13-16°C.	Optimum between 21°C and 25°C. Slower rate than C. monilifera at 13-16°C.
Seed Treatment	Faster rate and higher total germination if pericarp removed or seeds weathered.	Little germination unless seed coat cut or softened by boiling water or weathered.
Osmotic potential	Germination at -1.0 MPa only if pericarp removed. Lower germination than A. longifolia at -0.5 to -1.0 MPa.	Higher germination of treated seeds at -0.5 to -1.0 MPa than C. monilifera .

Chapter 5

Population dynamics of seedlings of
Chrysanthemoides and Acacia

"The form, tolerances, and persistence of species may be profoundly
modified by the proximity of neighbours of the same or other species.
It follows that the characteristics of individual species shown by
isolated individuals or pure populations may offer no significant
guidance to their behaviour in the presence of others."
(Harper 1964)

"It is not unreasonable therefore to describe the events preceding
ruderal dominance as a race between seedlings, the outcome of which
is measured in terms of relative seed output and is mainly determined
firstly by the frequency, size and germination characteristics of
contending seed populations and secondly by the growth-rates and
morphologies of the seedlings and established plants."
(Grime 1979)

5.1 Introduction

The ideal species for comparative demographic studies should be (1) closely related, (2) very common, (3) living in the same area within an extensive and stable ecosystem, and (4) representative of contrasting life-cycle strategies (Sarukhan & Harper 1973). This ideal is difficult to realise but C. monilifera and A. longifolia at least approach it in specifications 2, 3 and 4 above.

Mature plants of both these species are very common in the study area, as are seedlings of C. monilifera, but those of A. longifolia are common only in previously burnt areas. Nevertheless, emphasis was placed in this study on the population dynamics of seedlings of both species. Harper (1965) has advocated that seeds and seedlings of invading species should be looked at particularly closely and fluctuations in births and deaths of seedlings are more likely to be greater than of adults during a relatively short period.

Although climatic conditions can vary markedly from year to year and it would be preferable to follow individuals until reproductive maturity, time permitted seedlings to be studied only from 1979 to 1982. The aim was firstly to estimate seedling numbers of C. monilifera and A. longifolia in various positions from fore-dune to swale and secondly to examine their survivorship as influenced by density, time of year, dune position and light intensity.

5.2 Experiment 1

5.2.1 Methods

In order to estimate seedling numbers, I laid out five transects at random in August 1980 at Moruya. Each transect ran from the fore-dune to the swale and was permanently marked so that 25 quadrats each 0.5 x 0.5 m could be relocated at 1 m intervals along it. Observations were made from August 1980 to May 1982. Three transects were burnt in an accidental fire in October 1980.

5.2.2 Results

Initial densities of mature plants of C. monilifera and A. longifolia in the unburnt area were 0.30 and 0.17 m^{-2} respectively; in the area subsequently burnt they were 0.10 and 0.16 m^{-2} respectively. After the fire, no mature A. longifolia remained but 0.03 plants m^{-2} of C. monilifera resprouted from the base along the stems. Densities of mature plants in the unburnt area at the end of the study were 0.30 m^{-2} of C. monilifera and 0.15 m^{-2} of A. longifolia.

Results were not analysed statistically because of the unplanned fire and because only two transects remained in the unburnt area. However, it was evident that seedlings of C. monilifera were more numerous in the unburnt area and of A. longifolia in the burnt area (Table 5.1) and statistics were probably unnecessary to confirm this. Seedlings of C. monilifera occurred more frequently on the mid-dune than other positions while those of A. longifolia were found mainly on the swale and mid-dune.

More vigorous growth of seedlings occurred in the burnt transects so that by the end of 1981 they were larger than those in unburnt transects. Some plants of C. monilifera in the burnt transects, particularly those which had emerged at low densities, flowered and set seed within 12 months. Plants of C. monilifera originally present as seedlings ($\leq$6 leaves) did not flower in the unburnt transects, nor did A. longifolia even in the burnt area. Some leaf damage on A. longifolia by chewing insects and white fly larvae was evident.

5.2.3 Discussion

Numbers of seedlings of C. monilifera were lower in the burnt than the control area which was probably due to fire affecting seeds near the soil surface (Chapter 4), as well as a lower initial density of mature plants in the burnt area. Nevertheless, C. monilifera outnumbered A. longifolia in the burnt area, despite a 10-fold increase in the density of the latter (Table 5.1). Seedlings recorded in experiment 1 were not marked so that births and deaths were confounded. Such events were thus dealt with separately in experiment 3.

Table 5.1 Mean number of seedlings m^{-2} of <u>C.monilifera</u> and <u>A.longifolia</u> at various times in burnt and unburnt permanent transects. Standard errors are given in parentheses

Date		Unburnt		Burnt	
------	------	<u>C.monilifera</u>	<u>A.longifolia</u>	<u>C.monilifera</u>	<u>A.longifolia</u>
August	1980	71.6 (18.2)	0.08 (0.04)	25.7 (10.4)	0.05 (0.03)
November	1980*	20.2 (9.6)	0.08 (0.04)	0	0
January	1981	40.4 (13.9)	0.08 (0.04)	0.3 (0.2)	0.4 (0.2)
March	1981	131.2 (24.5)	0.08 (0.04)	2.1 (1.1)	0.8 (0.4)
October	1981	90.5 (20.7)	0.05 (0.03)	1.2 (0.8)	0.7 (0.4)
January	1982	43.6 (14.2)	0.05 (0.03)	1.1 (0.7)	0.7 (0.4)
May	1982	101.3 (21.8)	0.05 (0.03)	1.3 (0.8)	0.7 (0.4)

*   Fire occurred in the previous month

Fire increased the growth and development of subsequent *C. monilifera* seedlings to the extent that some plants reached reproductive maturity within 12 months, the added seed input thereby increasing the potential population of *C. monilifera*. Even under glasshouse conditions in the absence of predation, *C. monilifera* reached maturity at least 12 months faster than *A. longifolia*.

In the unburnt area, it is likely that the growth of *A. longifolia*, when it did occur would be reduced by the presence of *C. monilifera*, in view of the interactions reported in Chapter 7 which would in turn be emphasised by the disparity in densities between the two species. This hypothesis was tested only in sown populations of both species (Chapter 7). It could also be tested in natural populations by comparing the level of survival of *A. longifolia* in mixtures with *C. monilifera* and in monocultures where seedlings of the latter were removed. However, the low densities of *A. longifolia* precluded such an experiment.

5.3 Experiment 2

5.3.1 Methods

I manipulated seedling numbers of *C. monilifera* in another series of plots, to compare seedling survival at varying plant densities. An area was selected at Moruya on the mid-dune near mature plants of *C. monilifera*, with seedlings at the two- to four-leaf stage. These were thinned to 25, 50, 100 or 200 two-leaf seedlings in each 0.25 m^2 plot. Positions of plants were recorded and monitored at 2 monthly intervals from August 1981 until September 1982. Any new seedlings were removed.

5.3.2 Results

Mortality increased with increasing plant density although overall mortality was comparatively low (Table 5.2). Percentage mortality was arcsine transformed before analysis (Sokal & Rohlf 1969). Mortalities at the two highest densities were significantly greater than those at the two lowest (ANOVA, $P \leq 0.05$).

Table 5.2 Seedling mortalities, of <u>C.monilifera</u> at four densities
            expressed as percentages of the numbers in August 1981

Density	% mortality					
(no. 0.25m^{-2})	Oct.'81	Dec.'81	Mar.'82	May '82	July '82	Sept.'82
25	0 a	0 a	0 a	0 a	0 a	0 a
50	0 a	0 a	0 a	0 a	10.0 a	10.0 a
100	2.5 a	5.0 a	16.3 b	24.4 b	35.0 b	44.8 b
200	6.3 a	8.8 a	26.3 b	37.2 b	47.2 b	55.2 b

Values in each column followed by the same letter are not
significantly different at p=0.05 (Duncan's multiple range test).

5.3.3 Discussion

Mortality of C. monilifera was density-dependent. Although this was not investigated specifically with A. longifolia, it is likely to be of less importance in this species because of lower densities, even in burnt areas (maximum number of seedlings of A. longifolia were 30 m^{-2} in a burnt area compared to 1100 m^{-2} of C. monilifera in an unburnt area). Numerous studies by Harper and co-workers have shown a similar density-dependent effect on early mortality of various species (Harper 1960, 1964, 1965; Harper & Chancellor 1959; Sagar & Harper 1960; Harper & McNaughton 1962; Cavers & Harper 1967).

Although mortality was comparatively low even at high densities, the duration of the experiment was limited to 13 months and mortality of some accessions in Experiment 3 continued up to 22 months. It is also likely that density-dependent mortality would be more pronounced in seedlings in a previously burnt area because of their size and faster rate of growth (as seen in Experiment 1).

5.4 Experiment 3

5.4.1 Methods

In order to examine seedling mortality more closely, I selected four plots at random along a transect in August 1979, in an area at Moruya where mature plants of C. monilifera and A. longifolia were present, with the constraint that each of four positions were represented - foot of fore-dune, fore-dune, mid-dune and swale (Fig. 5.1). Established seedlings of C. monilifera were present but none of A. longifolia appeared at any time. Consequently I selected a further three plots in February 1980 in which established seedlings of both species were present. These were found only on the mid-dune and swale. Following a new accession of seedlings of both species, I selected a further three plots in July 1980, one of which (plot 9) contained also established seedlings of A. longifolia (Table 5.3).

The plots, each 1.0 x 0.5 m, were marked by metal tubes. These were used on each recording occasion to relocate a plant plotter, which utilised a co-ordinate system with two rules perpendicular to each other to fix the position of any plant (Cullen, Weiss & Wearne 1978). Thus a census of births and deaths of plants could be

FIG. 5.1 a. Foot of fore-dune, showing seedlings of C. monilifera
            ssp. rotundata.

FIG. 5.1 b. Looking from the mid-dune towards the fore-dune,
showing <u>Banksia integrifolia</u> (top right), <u>Acacia
longifolia</u> (bottom right), <u>Lomandra longifolia</u>
(bottom left) and <u>Chrysanthemoides monilifera</u> ssp.
<u>rotundata</u> (middle and top left (arrowed), climbing
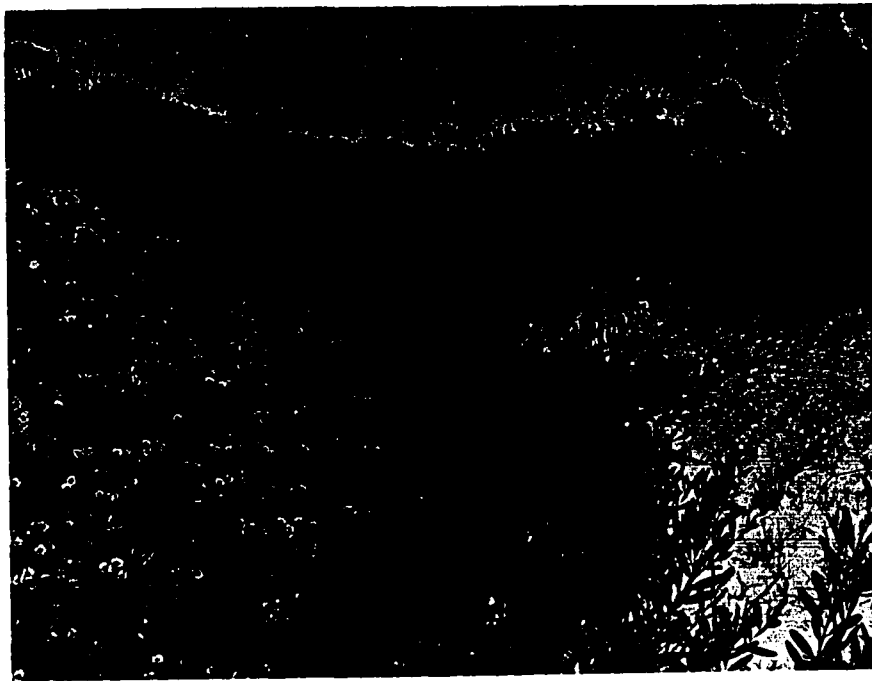through <u>B. integrifolia</u>).

FIG. 5.1 c. Swale area, looking towards the mid-dune, showing
Chrysanthemoides monilifera ssp. rotundata (left),
Acacia longifolia (middle) and Spinifex hirsutus
(right).

Table 5.3 Summary of plots in experiment 3 containing seedlings of
C. monilifera either alone or in mixtures with A. longifolia

Plot no.	Time of study	Light (%)	Species	Dune Position	Associated mature plants
1	August 1979 - May 1982	100	C.monilifera	Foot of fore-dune	C.monilifera immediately above on fore-dune
2	"	75	"	Fore-dune	C.monilifera and A.longifolia 1 m away
3	"	50	"	Mid-dune	Partly under C.monilifera; A.longifolia 2 m away
4	"	25	"	Swale	Partly under C.monilifera; A.longifolia 1.5 m away
5	February 1980 - May 1982	75	C.monilifera, A.longifolia	Swale (foot of slope)	C.monilifera and A.longifolia immediately above
6	"	75	"	Mid-dune	Partly under A.longifolia; C.monilifera 1.5 m away
7	"	75	"	Mid-dune	Partly under A.longifolia; C.monilifera 1.5 m away
8	July 1980 - May 1982	25	"	Swale	Partly under C.monilifera and A.longifolia
9	"	50	"	Swale	Under A.longifolia; C.monilifera 1 m away
10	"	25	"	Swale	Partly under C.monilifera and A.longifolia

established with more certainty than in Experiment 1.

At approximately monthly intervals plants were relocated and the number of leaves counted. Plants remained visible for some weeks after death so that most plants which had emerged but died between plotting intervals were recorded. Those plants present at the commencement of plotting were designated "established" seedlings and any subsequently appearing as "new" seedlings.

Light intensities in each plot were measured with a Lambda light sensor. Readings were made at mid-day at ten positions in each plot and the mean obtained. This was placed in one of four categories (25%, 50%, 75% and 100% of full sunlight), that designated being the one closest to the actual value (Table 5.3).

Statistical model

A model was fitted to the data to investigate the association between the distribution of the length of survival (ie. time to death) of a particular accession (whether "established" or "new" seedlings) and the factors species, dune position and light intensity.

The proportional hazards model used was first proposed by Cox (1972) and suggested for this study by R.B. Cunningham who used it to analyse conception time in beef heifers (Cunningham, Axelsen & Morley 1981). In this study, times to death of seedlings were grouped into monthly intervals to facilitate the use of a regression model which relates the probability distribution of time to death with explanatory variables (treatments were plot, position or light) describing the situation of each set of seedlings. The model requires no assumption about the form of the probability distribution of time to death. However, it does require an assumption that the risk of death relative to a standard value is constant at all times. This standard value (mortality rate) is multiplied by the treatment constants, from which the name "proportional hazards model" is derived.

If p_{ij} denotes the conditional probability that a plant in a particular plot (i) will die in a certain time interval (t_{j-1}, t_j), given that it had survived to that month ($j-1$), (that is, $p_{ij} = R/N$ where there are R deaths during a month out of N plants at the beginning of that month, R/N giving the actual probability of mortality), then Bartlett (1978) showed that the following linear

regression model may be obtained:

$$ln \left[- ln \, (1 - p_{ij}) \right] = \beta_i + \gamma_j$$

where γ_j are constants involving time to death and β_i are the treatment constants. The use of the conditional probability p_{ij} allows the assumption that the p's are conditionally independent. If the p's are regarded as being binomially distributed, this model belongs to the class of generalised linear models which can bè fitted using the computer program GENSTAT. In this way, values for γ_j for each month and β_i for each plot, position or light intensity were estimated. Further calculations enabled survival curves to be fitted. Standard errors of the differences between the curves were calculated using the computer program GLIM.

I carried out analyses on "established" seedlings on data from August 1979 to April 1981 and on "new" seedlings following a large accession in June 1980 until June 1981.

5.4.2 Results

C. monilifera

There was a good similarity between actual and fitted probabilities of survival of the 345 established seedlings recorded (shown for plot 1 in Fig. 5.2). The probability of survival was lowest between October and February in each of the first 2 years (Fig. 5.2). Numbers then stabilised in the following year when densities were lower (Fig. 5.3). Rainfall in the first October to February period totalled 312 mm and in the second 393 mm, with that in the intervening period only 192 mm (Fig. 5.4).

Survival probabilities of established seedlings in the swale, mid-dune and fore-dune were similar and markedly higher than at the foot of the fore-dune (Fig. 5.5), where burial was an obvious factor in mortality, the marker tubes being covered by c. 15 cm of sand in 1980.

Established seedlings in the lowest light category (due to a dense overhang of stems of parent plants) had a lower level of survival than those in higher light (Fig. 5.6).

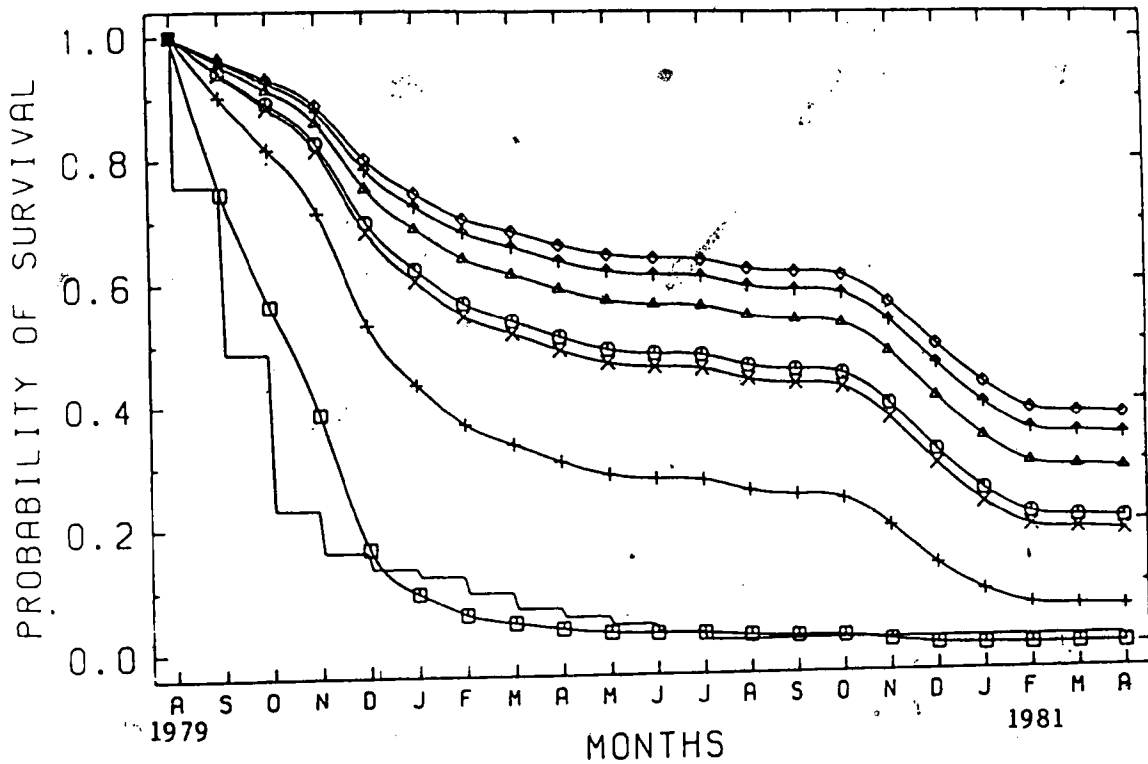FIG. 5.2. Probabilities of survival of established seedlings of
C. monilifera from August 1979 to April 1981 in plots
1 (□), 2 (O), 3 (Δ), 4 (+), 5 (X), 6 (◇), 7 (Φ), as shown
by fitted curves. The stepped line is the actual
probability of survival for plot 1.

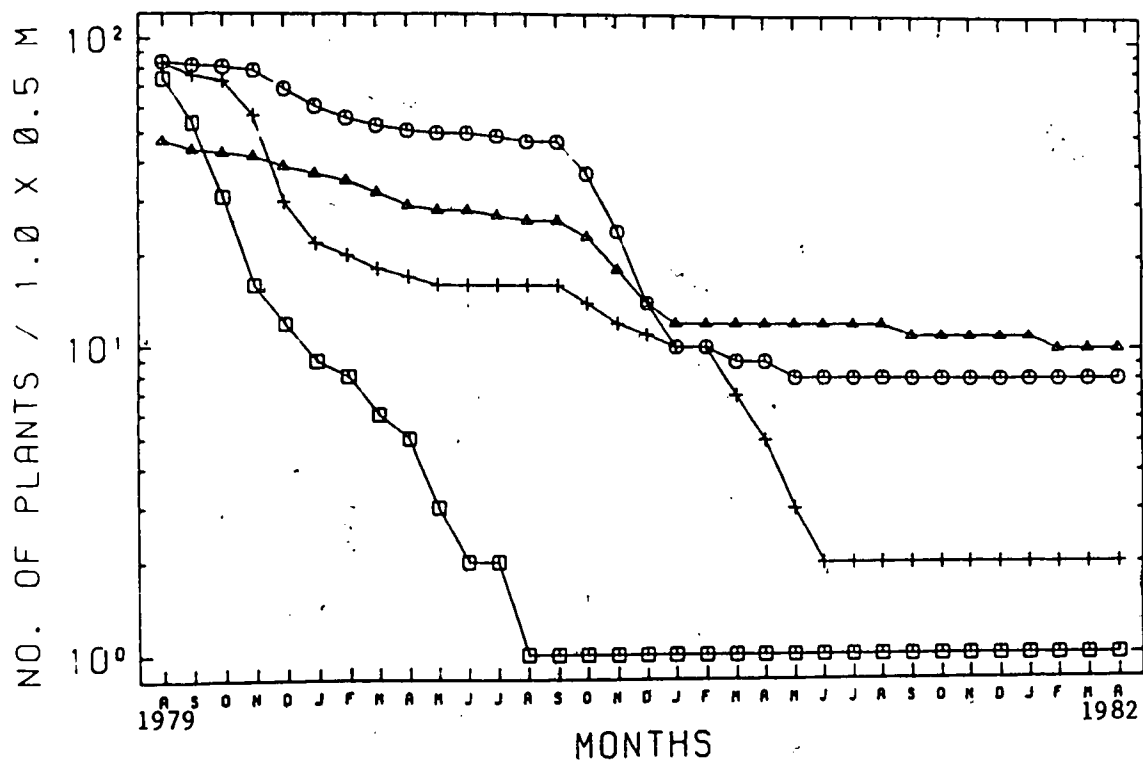FIG. 5.3. Density of established seedlings of C. monilifera
from August 1979 to April 1982 in plots 1 (□), 2 (0),
3 (Δ), 4 (+).
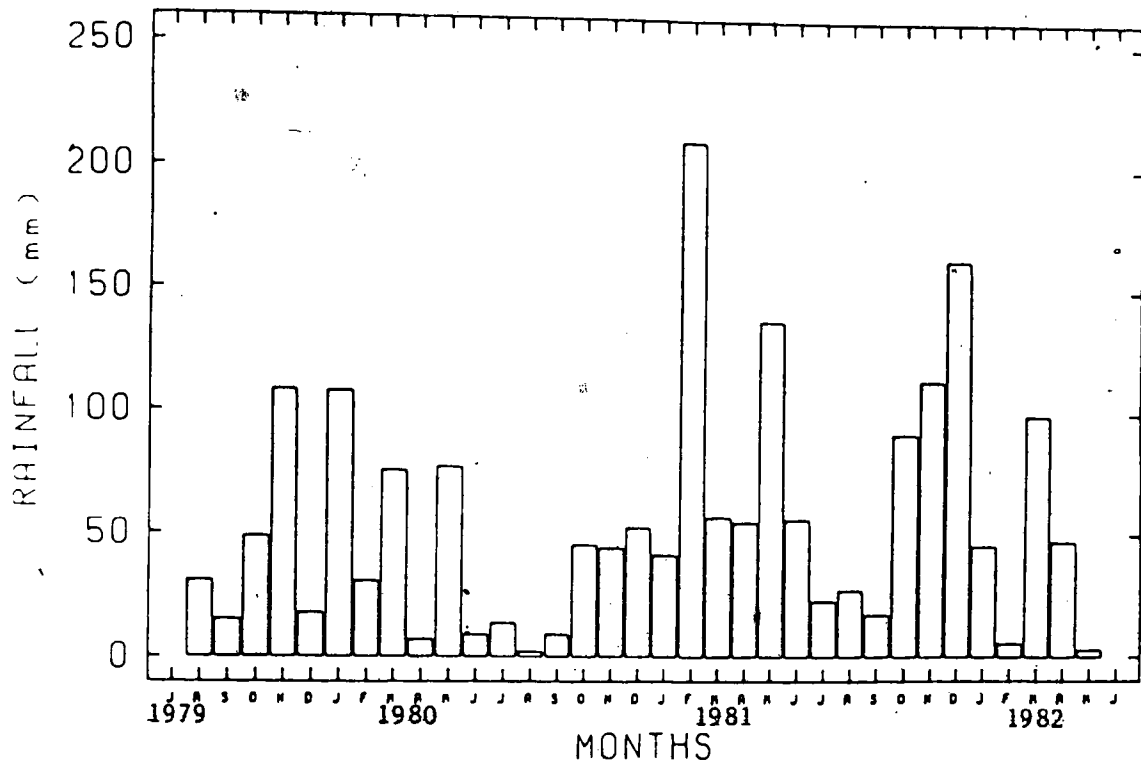
FIG. 5.4. Monthly rainfall at Moruya from August 1979 to May 1982.
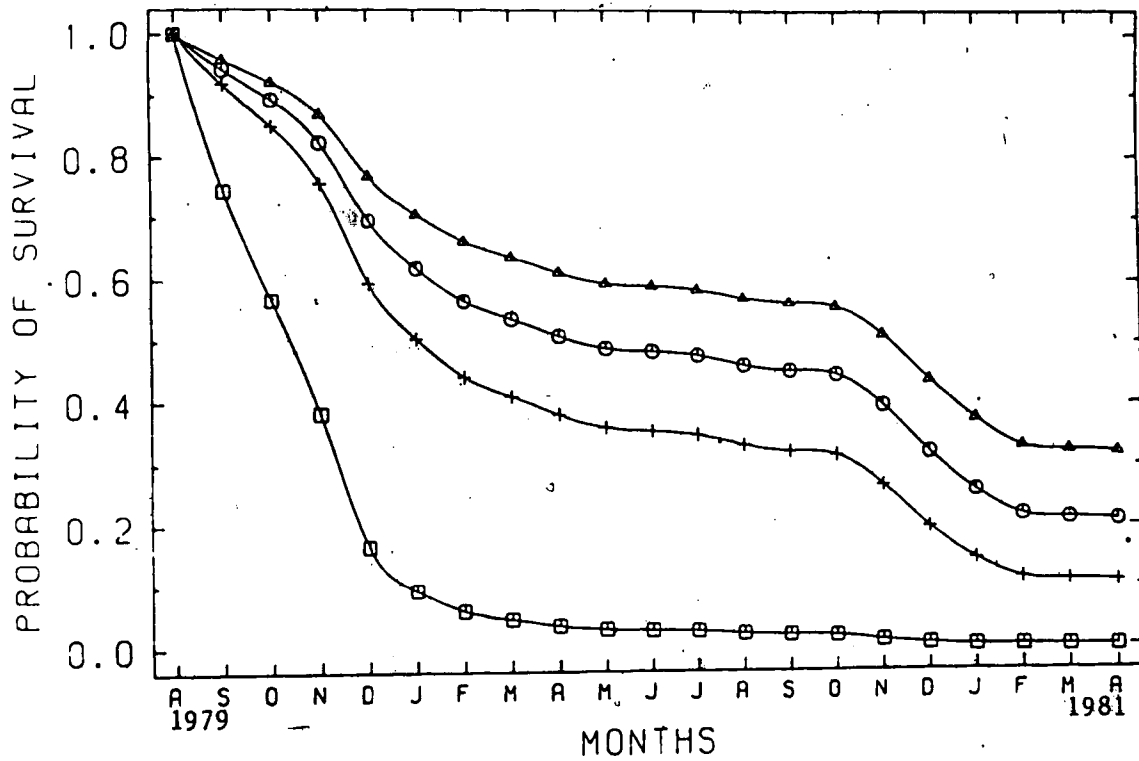
FIG. 5.5. Effect of dune position on probability of survival of
established seedlings of C. monilifera from August 1979
to April 1981. Positions are foot of fore-dune (□),
fore-dune (O), mid-dune (Δ) and swale (+).
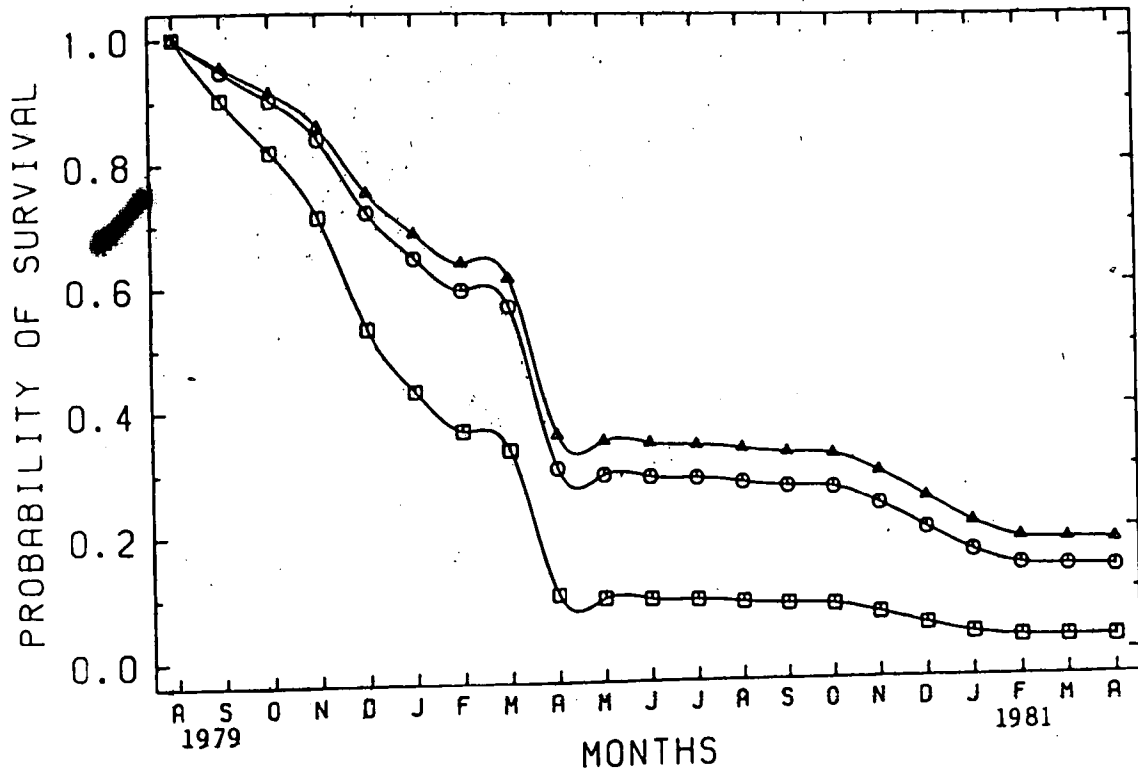
FIG. 5.6.   Effect of light intensity on probability of survival
of established seedlings of C. monilifera from August
1979 to April 1981.   Light intensity values are 25%
(□), 50% (O) and 75% (△) of full sunlight.
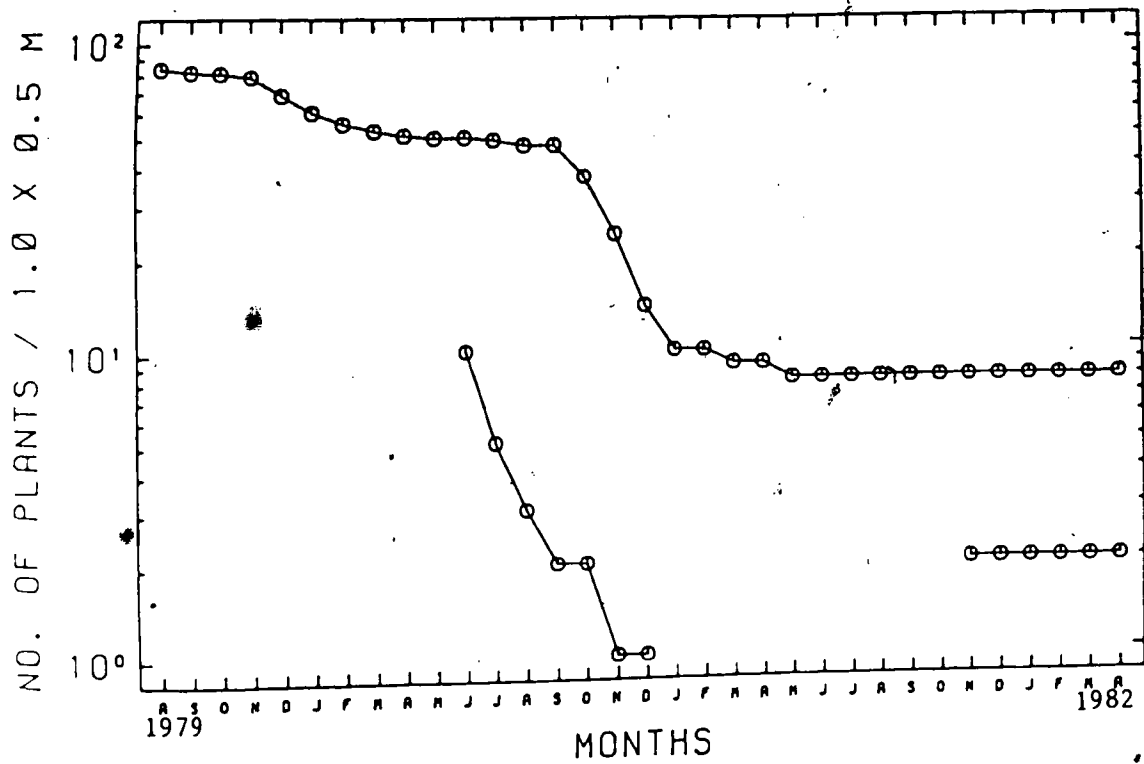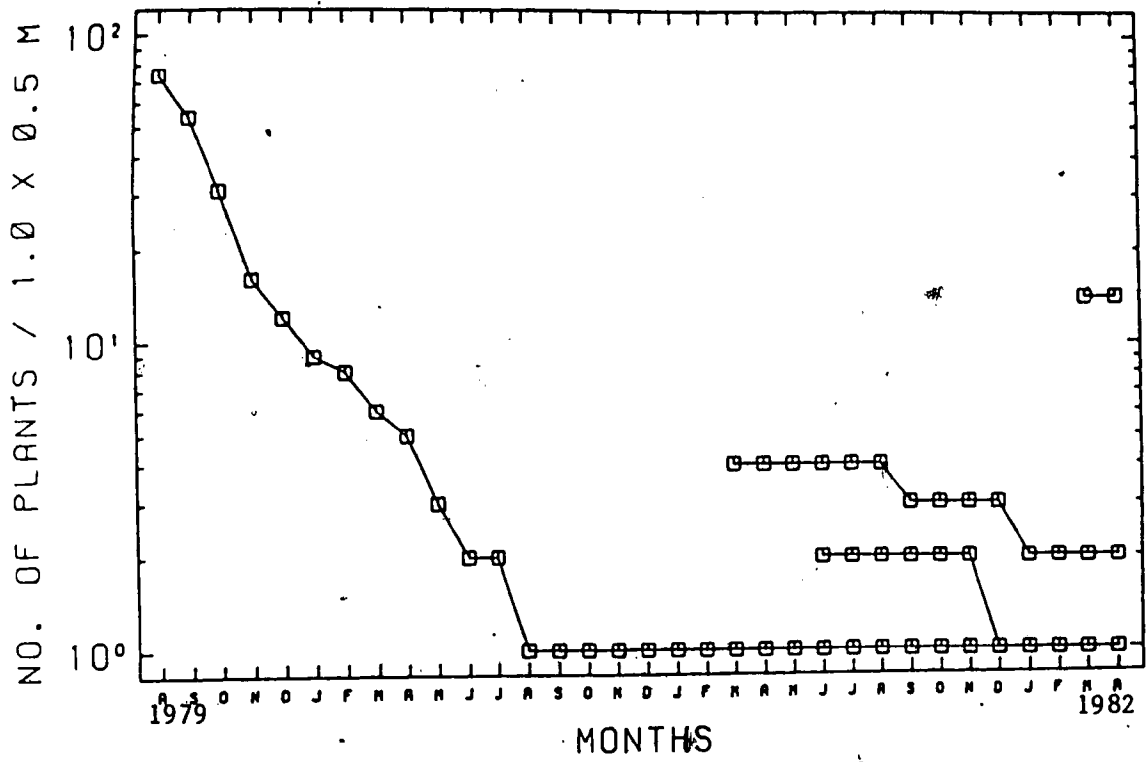
FIG. 5.7 a. Density of seedlings of C. monilifera from August 1979
to April 1982 in plot 1 (top) and plot 2 (bottom).
Established seedlings were present in August 1979.
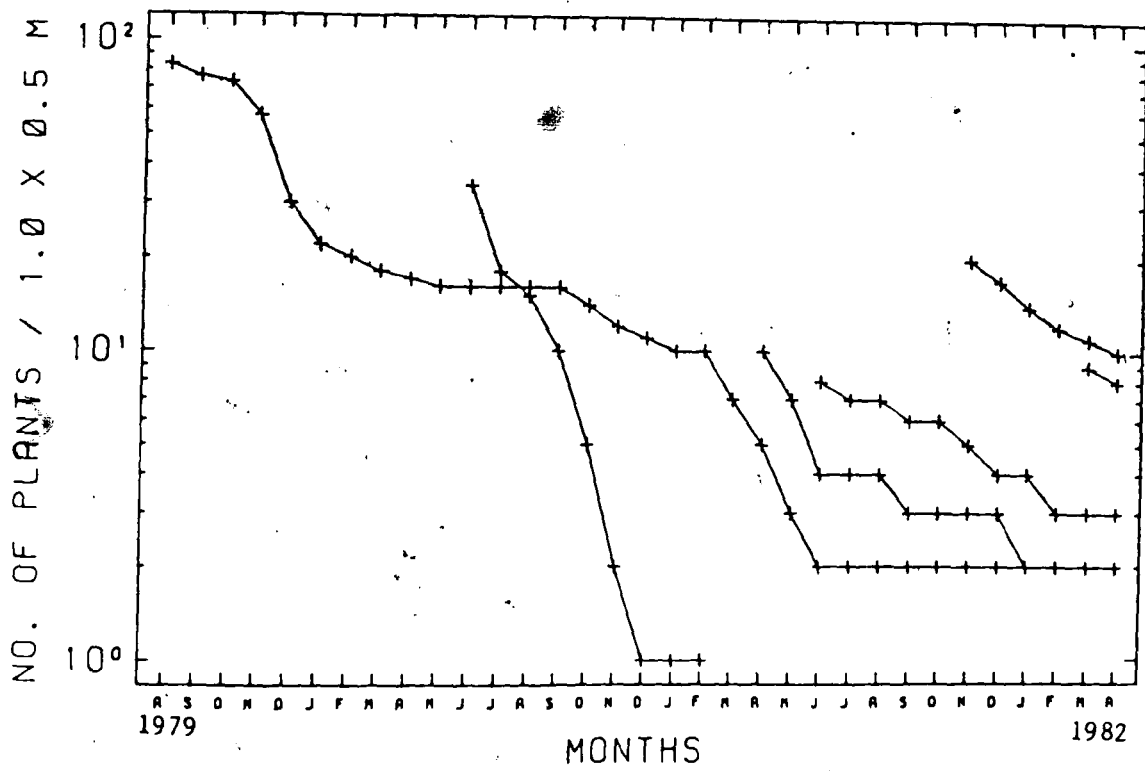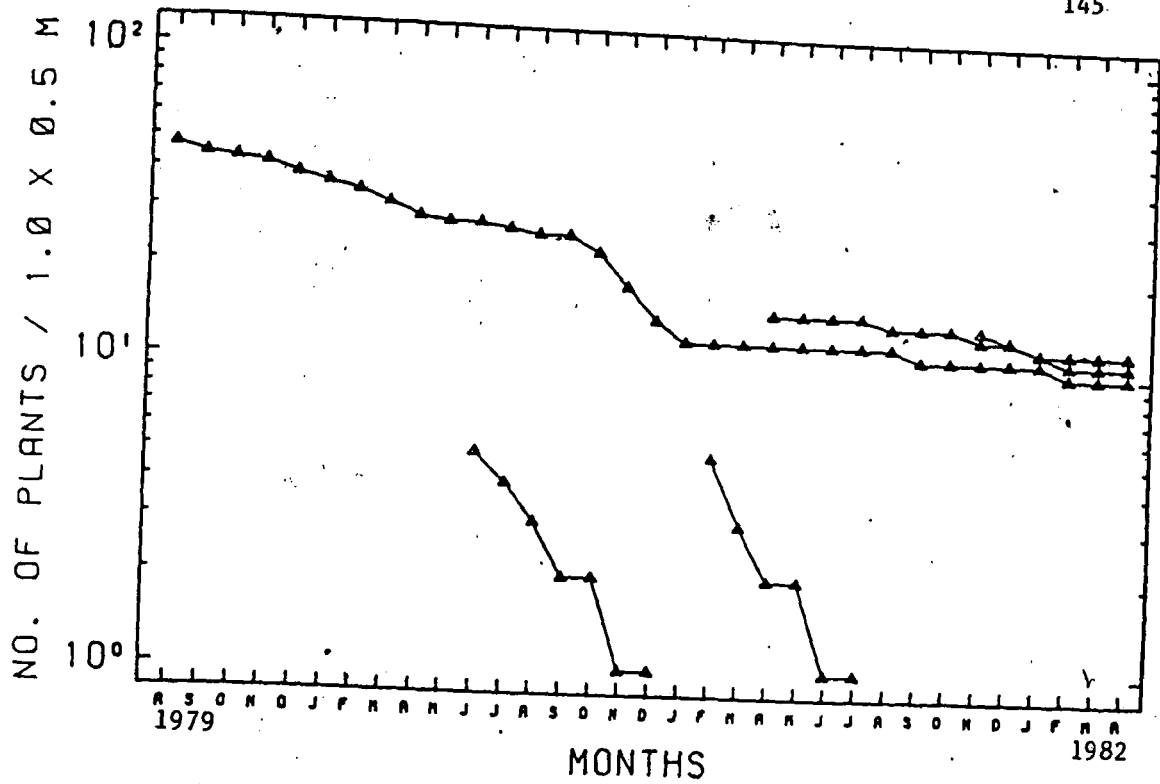
FIG. 5.7 b.   Density of seedlings of <u>C. monilifera</u> from August 1979
              to April 1982 in plot 3 (top) and plot 4 (bottom).
              Established seedlings were present in August 1979.
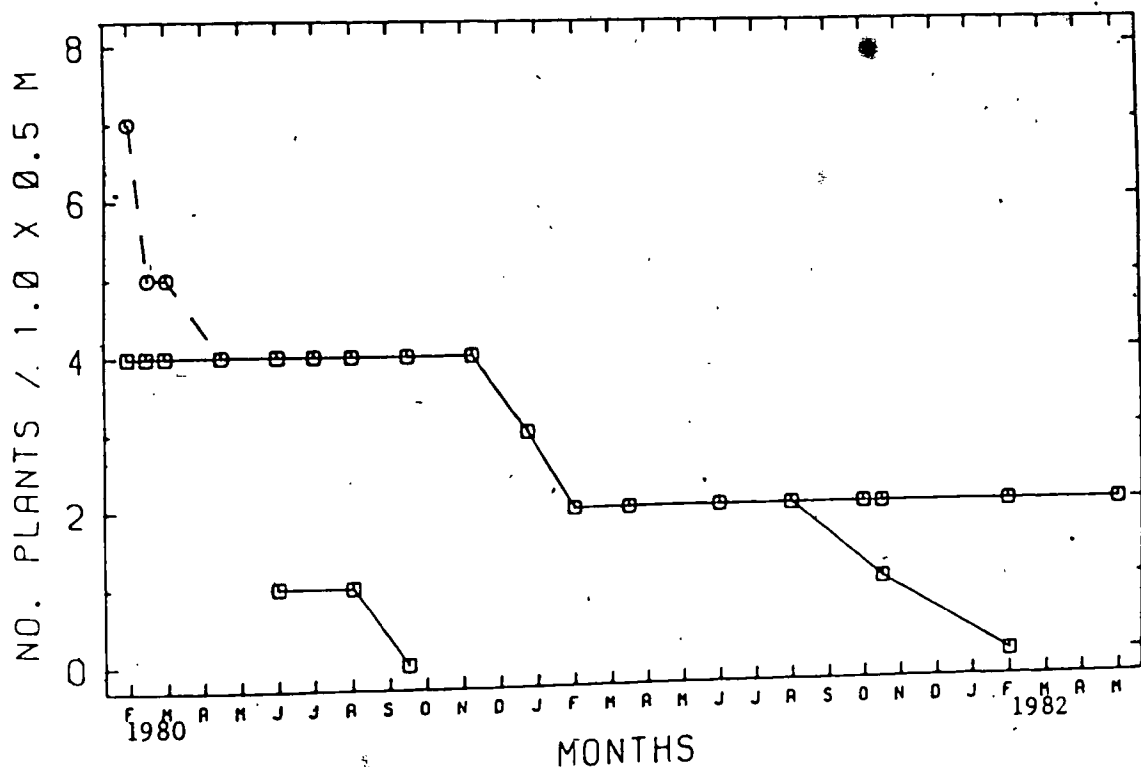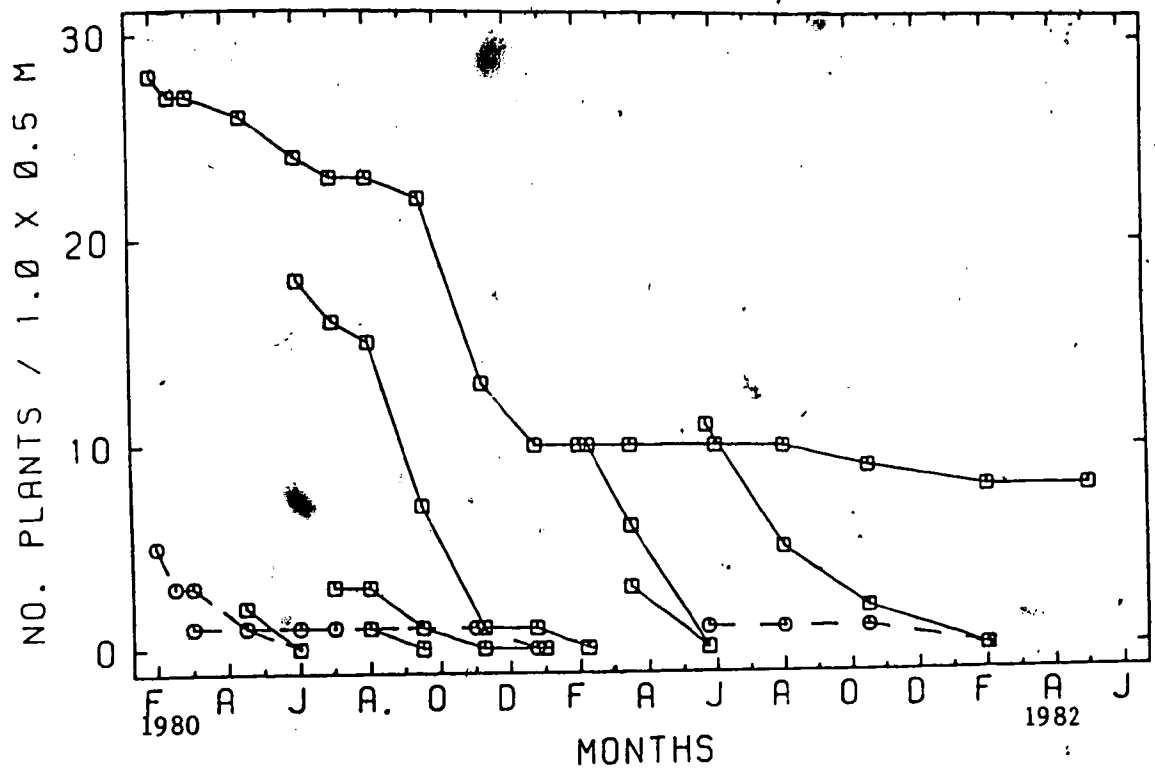
FIG. 5.8 a.   Density of seedlings of C. monilifera (□) and
A. longifolia (O) from February 1980 to May 1982
in plot 5 (top) and plot 6 (bottom). Established
seedlings were present in February 1980.
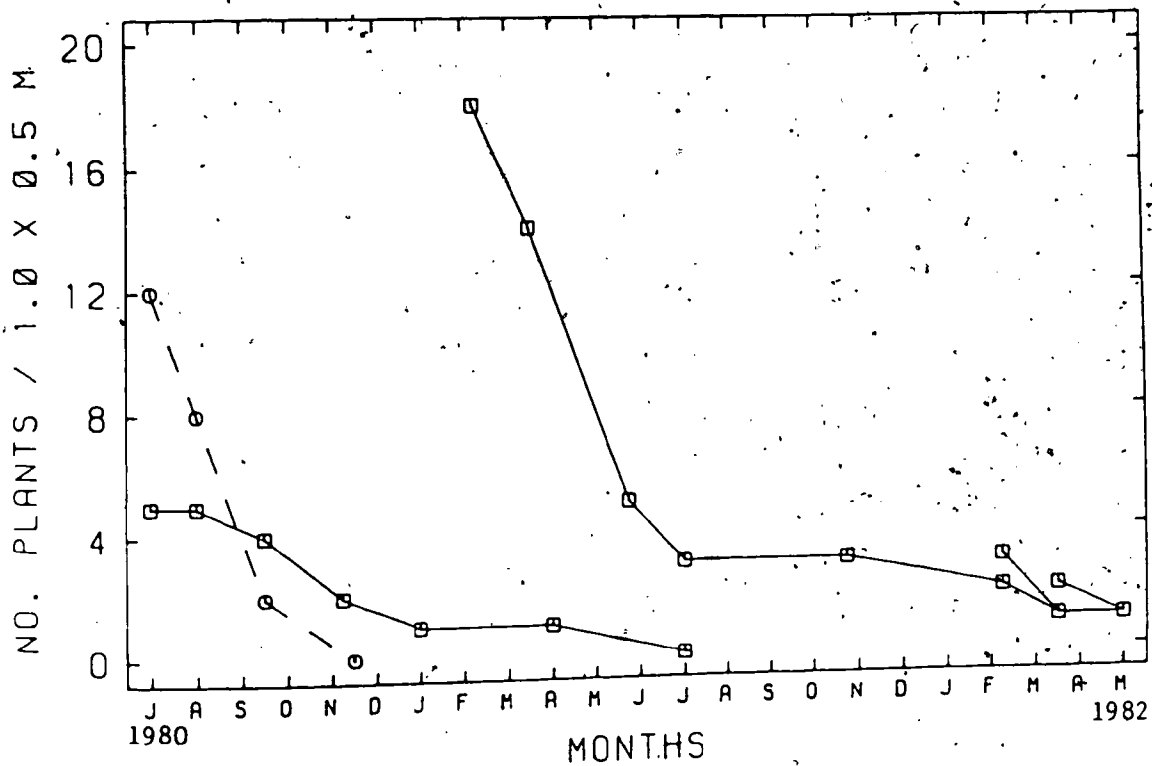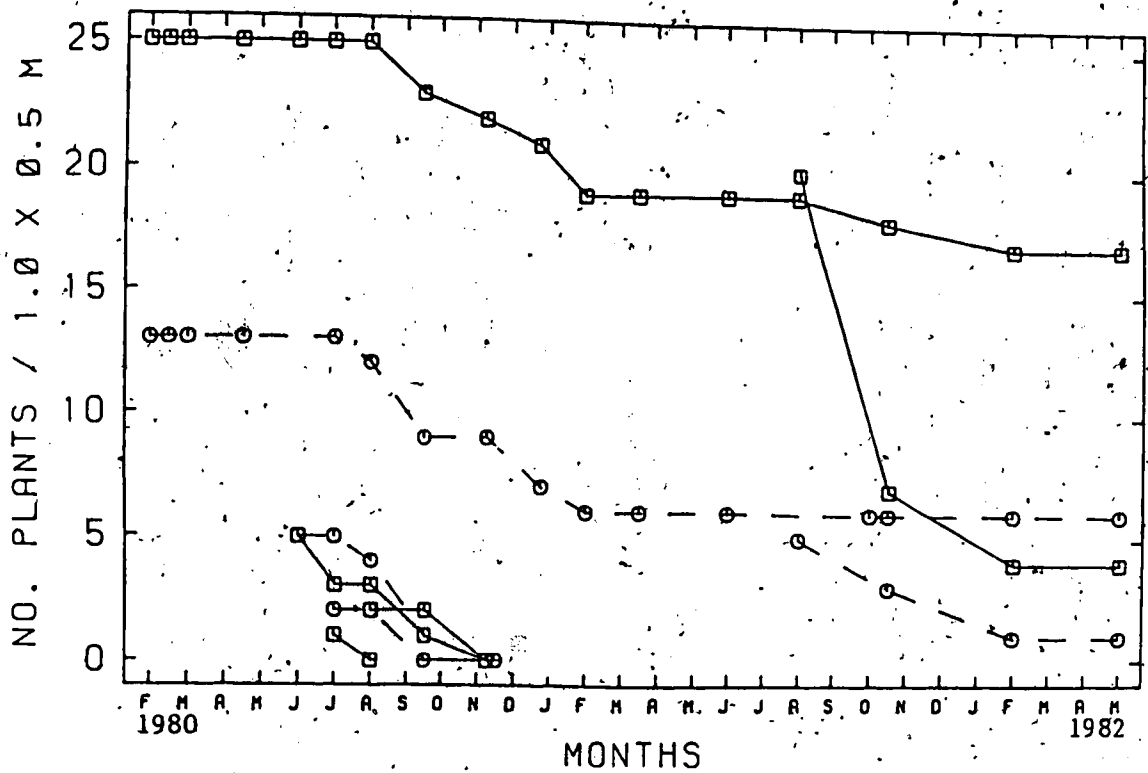
FIG. 5.8 b. Density of seedlings of C. monilifera (□) and
A. longifolia (O) from February 1980 to May 1982
in plot 7 (top) and from July 1980 to May 1982
in plot 8 (bottom). Established seedlings were
present in February 1980 in plot 7 but the first
accession of new seedlings in plot 8 emerged in
July 1980.
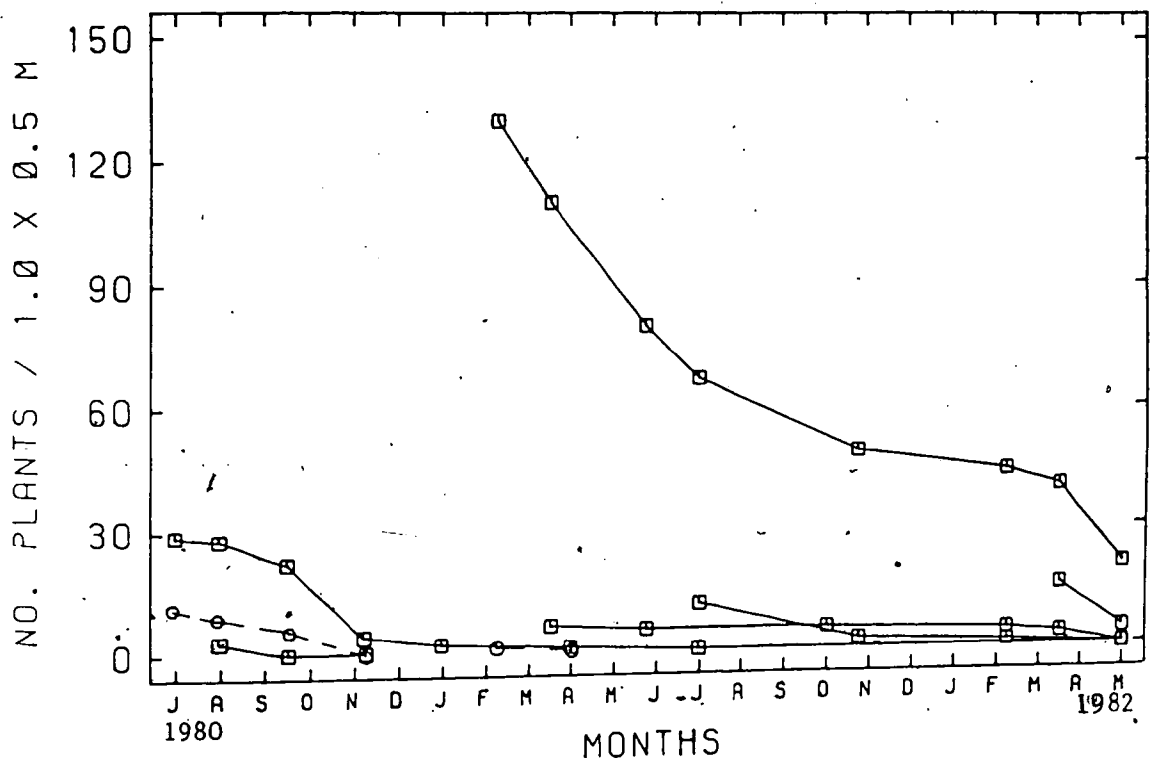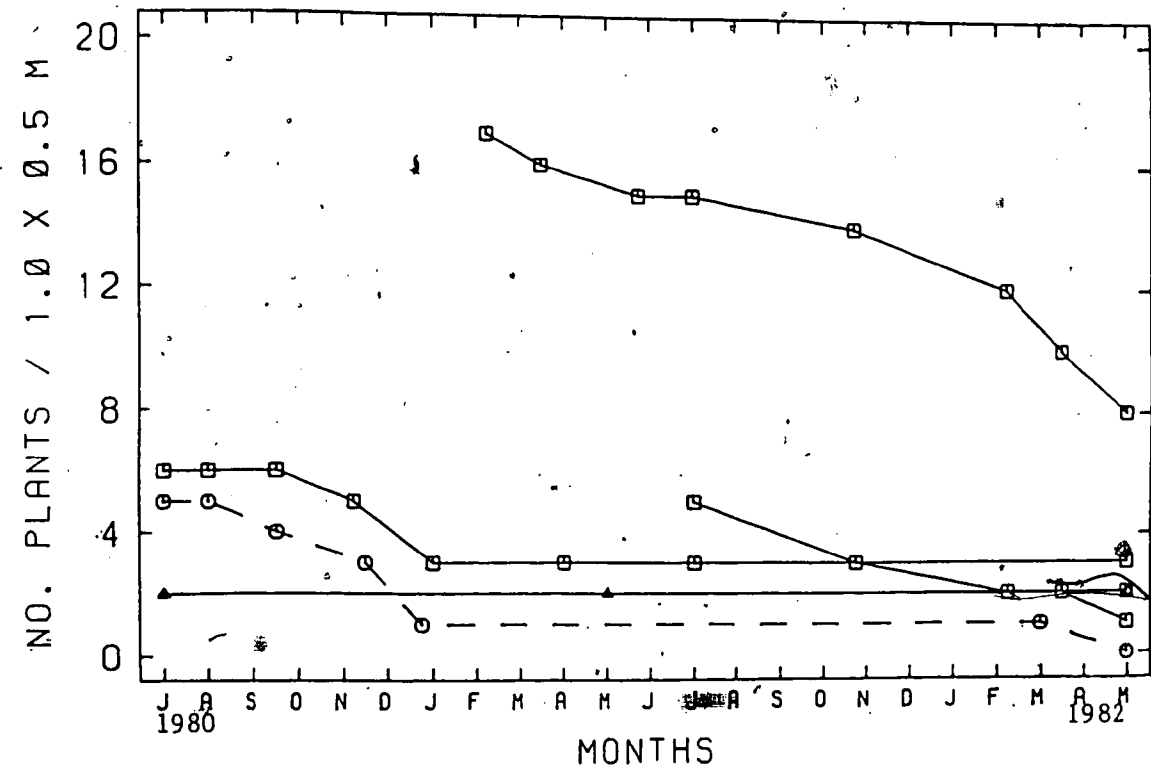
FIG. 5.8 c. Density of seedlings of <u>C. monilifera</u> (□) and
<u>A. longifolia</u> (O) emerged in 1980 and of <u>A. longifolia</u>
(△) emerged in 1979 in plot 9 (top) and plot 10 (bottom).
New seedlings of both species were present in July 1980.
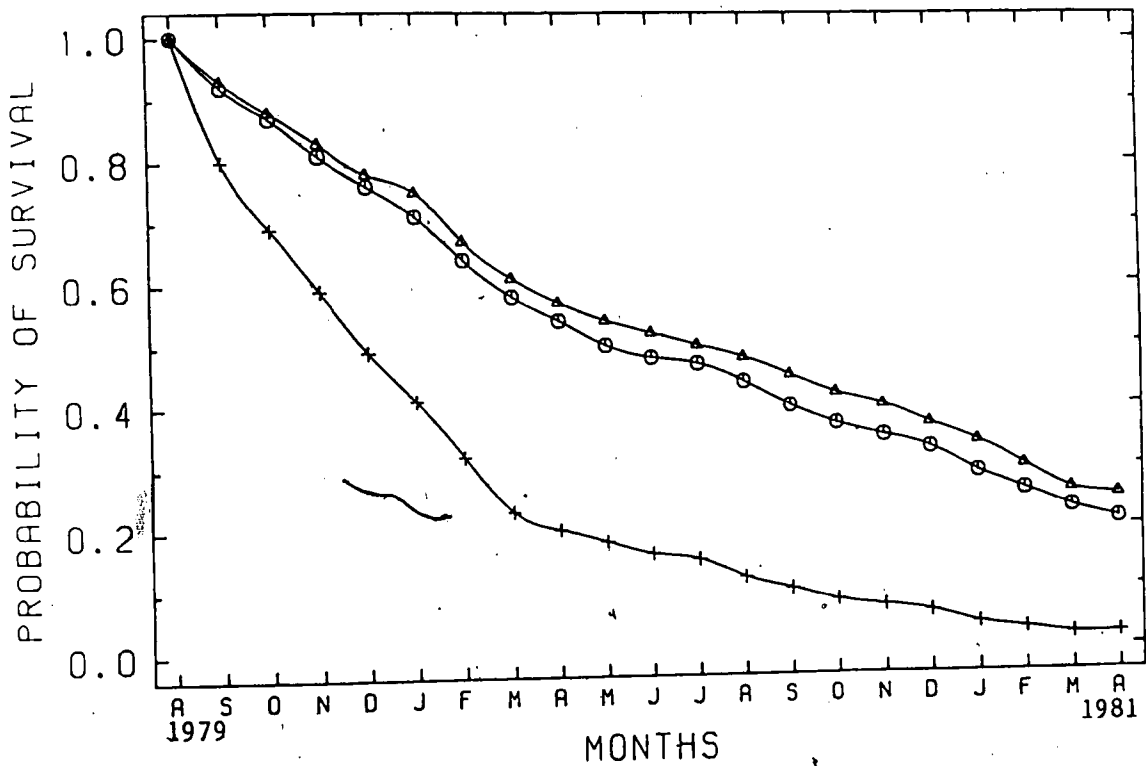
FIG. 5.9.   Effect of dune position on probability of survival of
established seedlings of A. longifolia. Positions are
swale (+) and mid-dune (plot 6, Δ and plot 7, 0).

There were 440 "new" seedlings of C. monilifera recorded during the study. The level of mortality of most accessions was higher than that of established seedlings, particularly in plots 2, 3, 5, 6, 7 where the level of mortality of the latter was comparatively low (Figs. 5.7, 5.8).

The June 1980 accession (following 77 mm of rain in April 1980) suffered a higher level of mortality than some other accessions (Figs. 5.7, 5.8). However, only 33 mm of rain fell from June to September 1980 (Fig. 5.4). There were no apparent relationships in the June accession between probabilities of survival and position or light. Not all plots had new accessions at similar times subsequently, so further comparisons between positions and light were not made.

A. longifolia

There were only 25 "established" seedlings of A. longifolia recorded. The probability of survival of A. longifolia followed a steady decline with time (Fig. 5.9), compared with the generally low level of mortality of C. monilifera between March and September 1980. However statistical comparisons were not made because of the low numbers of A. longifolia.

There was a trend towards a lower level of survival of A. longifolia (as with C. monilifera) in the swale than on the mid-dune (Fig. 5.9). Sand drift from the mid-dune buried some seedlings in the swale at various times.

There were 50 "new" seedlings recorded. As with C. monilifera, there was a low level of survival of the June 1980 accession, both in the swale and mid-dune (Fig. 5.8).

5.5 Discussion and summary

There was a comparatively low level of seedling survivorship of both C. monilifera and A. longifolia which agrees with the low level of juvenile survivorship of most pioneer and colonising species (Harper 1965). There were a number of factors associated with this in the present study:

1. The low level of survivorship of the June 1980 accession of new seedlings was associated with low rainfall. The high

transpiration rate and high densities of C. monilifera (Chapter 9) would also tend to deplete soil moisture in the root zone, leaving little for A. longifolia. A similar situation occurred in glasshouse experiments where survival of A. longifolia was greater under water stress in monocultures than in mixtures with C. monilifera (Chapter 7). Soil moisture would tend to be further depleted both by increasing evaporation and transpiration rates (Chapter 9) in the warmer months, which corresponded to a period of low levels of survivorship.

2.   Burial of seedlings by sand in the swale and at the foot of the fore-dune was an obvious cause of mortality at some times.

3.   Low light conditions contributed to the level of mortality, at least of C. monilifera. Light intensity underneath mature C. monilifera was generally low but very variable (from 2% to 60% of full sunlight under the one plant). Mature A. longifolia had a more open canopy but light intensity underneath was again variable (from 5% to 70% of full sunlight). Hence the level of mortality of individual seedlings in relation to light depended very much on their position in relation to mature plants.

4.   The level of survivorship was generally greater in established than in new seedlings. This may have been partly due to greater root development in the former, enabling seedlings to draw on the greater amount of moisture which was usually present deeper in the soil (Chapter 9).

        This type of survivorship (with the level of mortality highest in the young stages) has been classified Type III (Deevey 1947). In Ranunculus spp., a concave survivorship or Type III curve lasts for 20-30 weeks before the population acquires a linear survivorship or Type II curve and constant half-life (Sarukhan & Harper 1973). However, even then when survivorship is linear over years, rate of mortality shows seasonal periodicity. The highest level of mortality of Ranunculus spp. occurs when survivors are making maximal growth, rather than in a time of harsh environment. A similar situation appears to exist in established seedlings of C. monilifera in that the level of mortality is generally greatest in the spring-summer period, when maximum shoot growth occurs (Chapter 6).

5.   Predation of seedlings of both species was uncommon in the study area except for an occasional attack by leaf-eating

insects. However, in the case of <u>A. longifolia</u>, this may have been associated with low density, making individuals difficult to locate. Where seeds were sown in the open and seedlings of <u>A. longifolia</u> were subsequently present at densities of c. 100 m^{-2}, predation was often observed and defoliation was a major factor in mortality.

The generally low level of seedling survivorship of <u>C. monilifera</u> is not greatly disadvantageous because:

(a) The risk of mortality of adults, even after fire, is comparatively low.

(b) There is an extended period of seed production and seed fall during the year (Chapter 3).

(c) The level of seed predation is comparatively low (Chapter 3).

(d) The number of seeds per plant and subsequent seedlings produced are high.

On the other hand, the low level of survivorship of new and established seedlings of <u>A. longifolia</u> is particularly disadvantageous because:

(a) The risk of mortality of adults due to fire and, to a lesser extent, insect damage, is high.

(b) There is only a comparatively short period of seed production and seed fall during the year (Chapter 3).

(c) The level of seed predation is comparatively high (Chapter 3).

(d) The number of seeds per plant and subsequent seedlings produced are low.

Chapter 6

Growth of Chrysanthemoides and Acacia

"It is hoped that this Symposium may stimulate more interest in the interaction between exotits and native vegetation. In particular, comparisons of native species and exotics in terms of genotype, environmental and nutrient requirements, growth form, growth rate, reproductive capacity, protection from grazing, resistance to pests and diseases, allelopathy etc. ... are required."
(Amor & Piggin 1977)

Introduction

The preceding chapters provide information on factors affecting the ecology of C. monilifera and A. longifolia from the stage of the seed pool, seed germination and seedling growth through to flowering and seed production. I used information from these chapters to prepare life tables for C. monilifera and A. longifolia since this could help explain the invasive ability of C. monilifera in Australia in terms of population increase. Inferences may also be derived from a study of these tables as to the relative performances of the above species in the field. I tested such predictions by comparing the two species in their seedling growth and in their shoot growth when plants were established.

6.1 Life tables
6.1.1 Introduction

The use of life tables for various weedy species has been outlined by Sagar & Mortimer (1976), to help understand the population dynamics of weeds. Mature individuals in a given generation may, besides surviving themselves, contribute to an increase in the population from genet or seed reproduction (Kays & Harper 1974). The route by which this is carried out may be divided into five main intermediate phases:

(a) number of seeds produced (P in chapter 3, section 3.2);

(b) number of seeds falling on the soil surface (seed rain) (W in chapter 3) plus invading seeds;

(c) number of seeds in the soil seed bank, including "carry-over" from previous generations;

(d) number of seedlings; and

(e) number of established juvenile plants.

Between each of these and between juveniles and adults are interphases which determine the number in each phase, e.g. the probability that a seed will give rise to a seedling.

Ramet or vegetative reproduction is relatively unimportant with the species in this study except in the case of fire after which mature plants of C. monilifera may survive both from basal resprouting

and from dormant buds along the prostrate stems, producing daughter plants. I therefore compared numbers both in unburnt and burnt situations.

6.1.2 Methods

Estimates of seed production, size and fate of the soil seed pool and densities of seedlings and mature plants were obtained from data in Chapters 2-5 and 10. Density of mature plants was also estimated by the point-quarter method (Cottam & Curtis 1956) and a mean value obtained. Values per plant could then be converted to values per unit ground area. The buried seed bank included a previous seed bank of dormant seeds. The losses from the buried seed bank were the difference between it and the sum of seedlings and dormant seeds. Dormant seeds then became the "carry-over" in the following year. They were estimated from seed viability values after 12 months given in Chapter 3, multiplied by the input to the seed bank (W). Regeneration of mature plants after fire was estimated from the results in Chapter 10 and by counting numbers of dead and resprouted plants in 20 areas, each 5 m x 5 m, for 12 months after a wild-fire in October 1980.

Since seeds of C. monilifera were dispersed mostly by birds such as currawongs, at least at the study site, an estimate of the number of seeds immigrating into an invaded area was obtained by counting the number of surface seeds on the ground in 100 random 1 m^2 quadrats where mature plants of C. monilifera were absent and assuming similar seed drop occurred in already invaded areas.

6.1.3 Results

In the life tables for unburnt areas, the potential population increase of C. monilifera (Fig. 6.1) is much greater than that of A. longifolia (Fig. 6.2). In the 3 years in which data were collected, plants of both species in the unburnt area went from the seedling to the established juvenile phase but had not yet flowered and set seed. Therefore no figure can be put on the interphase between juvenile and mature plants.

In a burnt area, most surface and shallowly buried seeds of C. monilifera were killed (Chapter 4), thereby reducing the probability of seeds in the soil producing a seedling (Fig. 6.3). However, survival of seedlings to the juvenile stage increased. To this must be added basal resprouting of original plants and daughter

FIG. 6.1. Diagrammatic life cycle for <u>C. monilifera</u> in an unburnt area.
Values for each phase (in rectangles) are given on a m^{-2}
yr^{-1} basis. Interphase values (in triangles) are fractions
surviving between successive phases except for the top
triangle which are number of seeds per plant. Dotted lines
represent losses from each phase.

```
                    ┌──────────────┐
                    │   MATURE     │
                    │   PLANTS     │ ----→ 0.005
                    │   0.05       │
                    └──────┬───────┘
                          ╲2400╱

                    ┌──────────────┐
                    │   SEEDS      │
                    │  PRODUCED    │ ----→ 60
                    │   120        │
                    └──────┬───────┘
                          ╲0.5╱

   ┌──────────┐     ┌──────────────┐
   │ INVASION │     │  INPUT TO    │
   │    0     │ ──→ │  SEED BANK   │ ----→ 54
   └──────────┘     │    60        │
                    └──────┬───────┘
                          ╲0.1╱

   ┌──────────┐     ┌──────────────┐
   │ PREVIOUS │     │   BURIED     │
   │SEED BANK │ ──→ │  SEED BANK   │ ----→ 6
   │    7     │     │    13        │
   └──────────┘     └──────┬───────┘
                         ╲0.004╱

                    ┌──────────────┐
                    │  SEEDLINGS   │
                    │    0.1       │ ----→ 0.09
                    └──────┬───────┘
                          ╲0.1╱

                    ┌──────────────┐
                    │  JUVENILES   │
                    │    0.01      │ ----→ 0.003
                    └──────────────┘
```

FIG. 6.2.   Diagrammatic life table for <u>A. longifolia</u> in an unburnt area.
Values for each phase (in rectangles) are given on a m^{-2}
yr^{-1} basis. Interphase values (in triangles) are fractions
surviving between successive phases except for the top
triangle which are number of seeds per plant. Dotted lines
represent losses from each phase.

FIG. 6.3. Diagrammatic life table for C. monilifera in a burnt area. Values for each phase (in rectangles) are given on a m^{-2} yr^{-1} basis. Interphase values (in triangles) are fractions surviving between successive phases. Dotted lines are rounded losses from each phase.
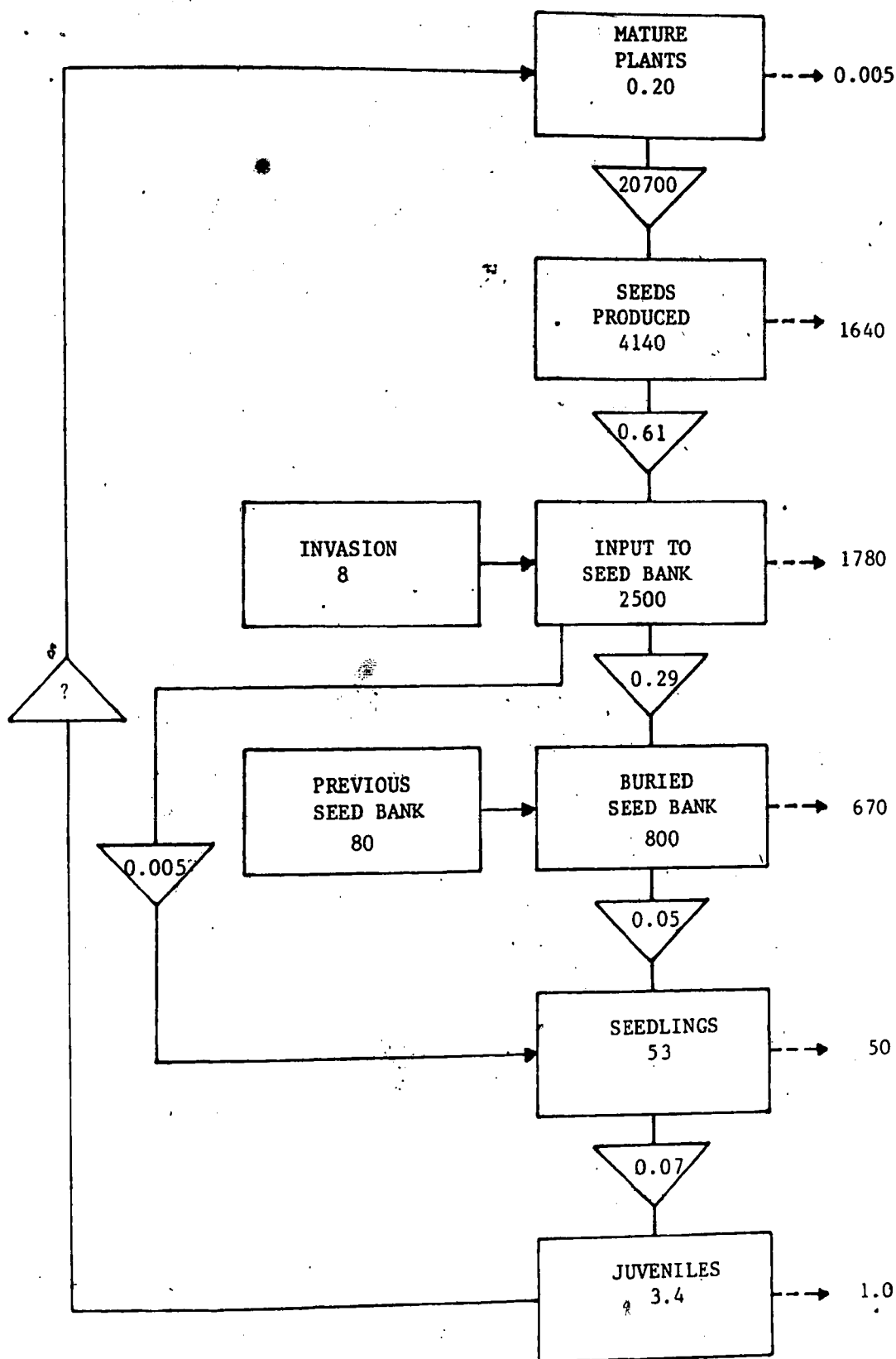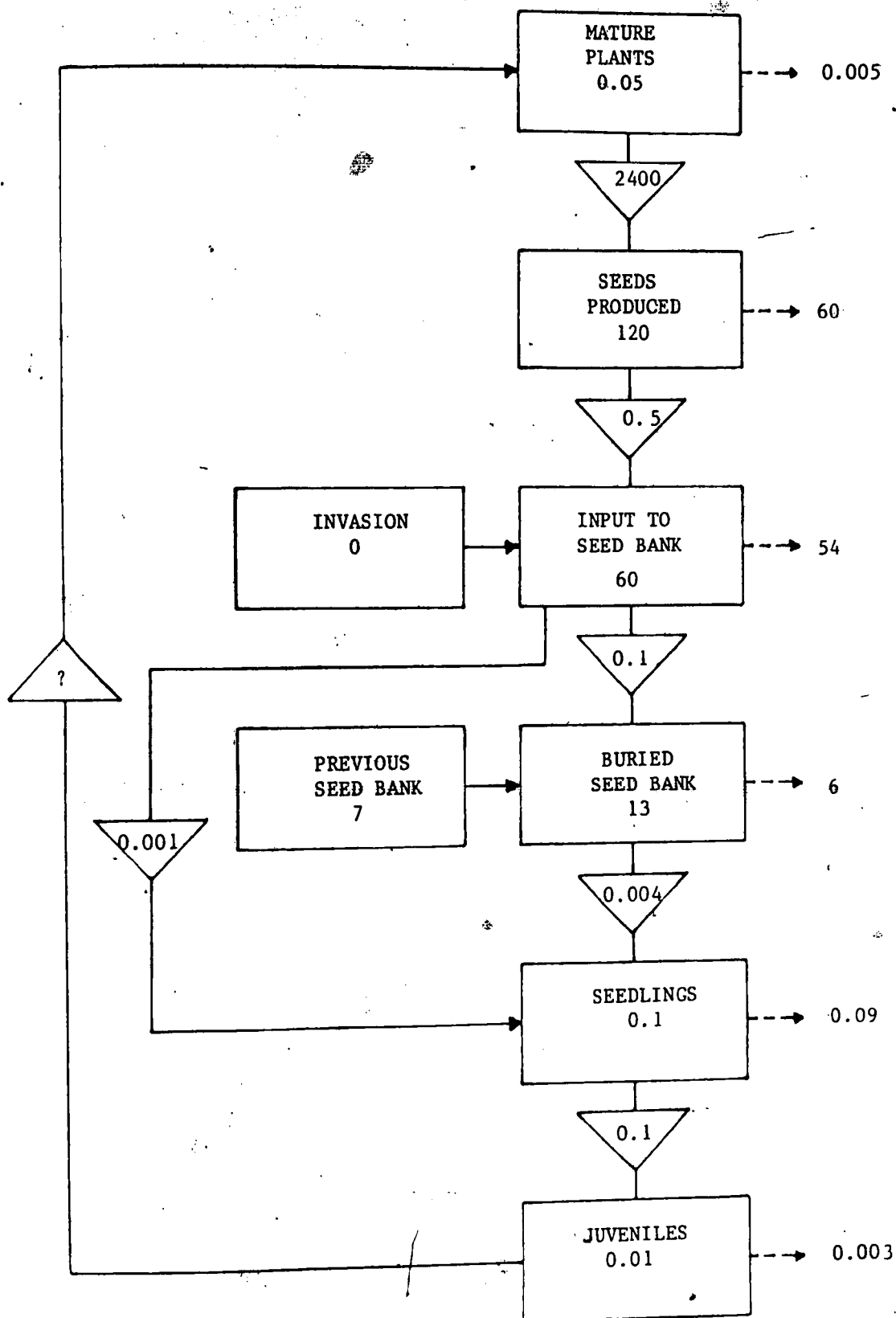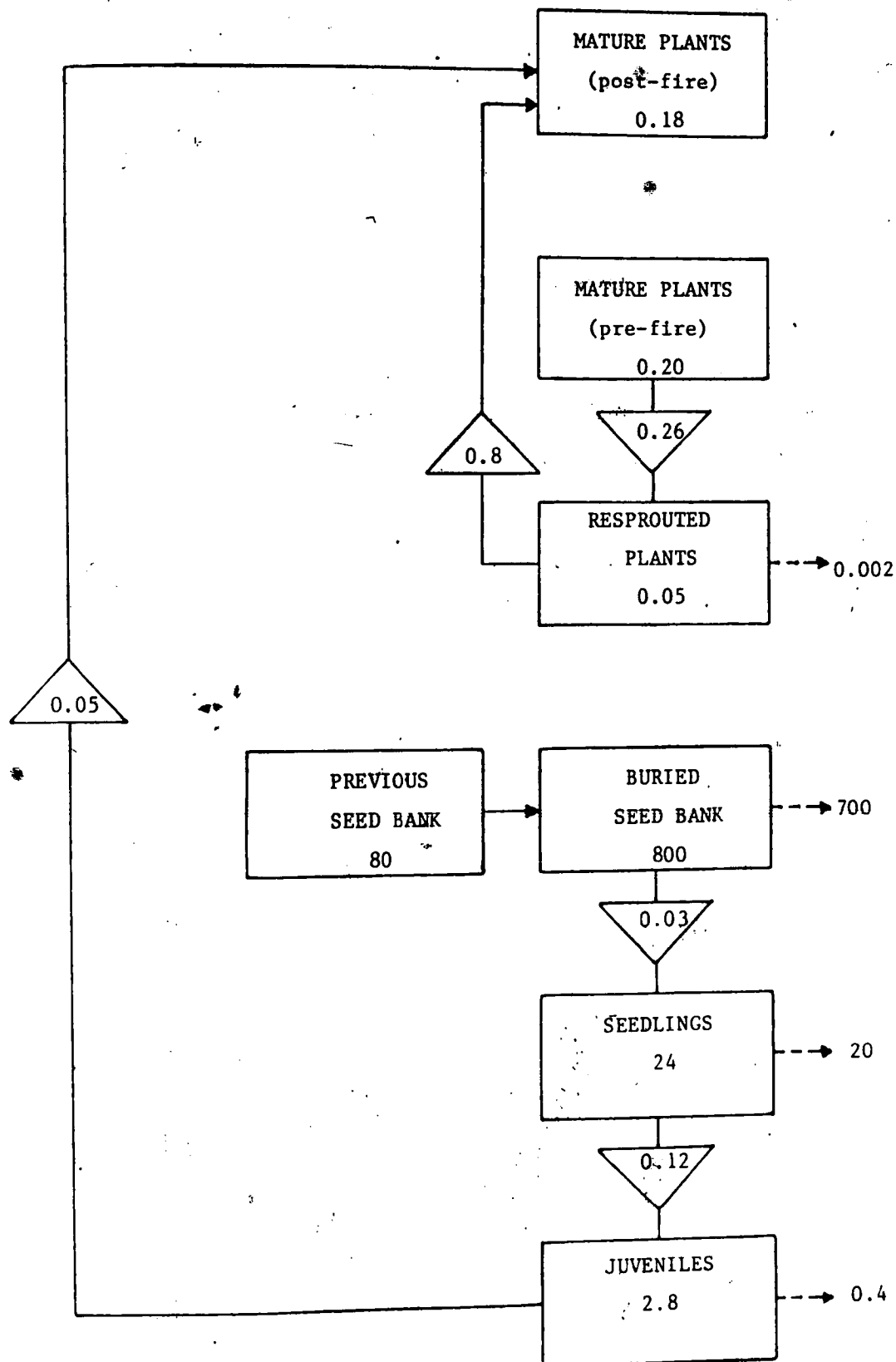
FIG. 6.4. Diagrammatic life table for A. longifolia in a burnt
area. Values for each phase (in rectangles) are given on
a m^{-2} yr^{-1} basis. Interphase values (in triangles) are
fractions surviving between successive phases. Dotted
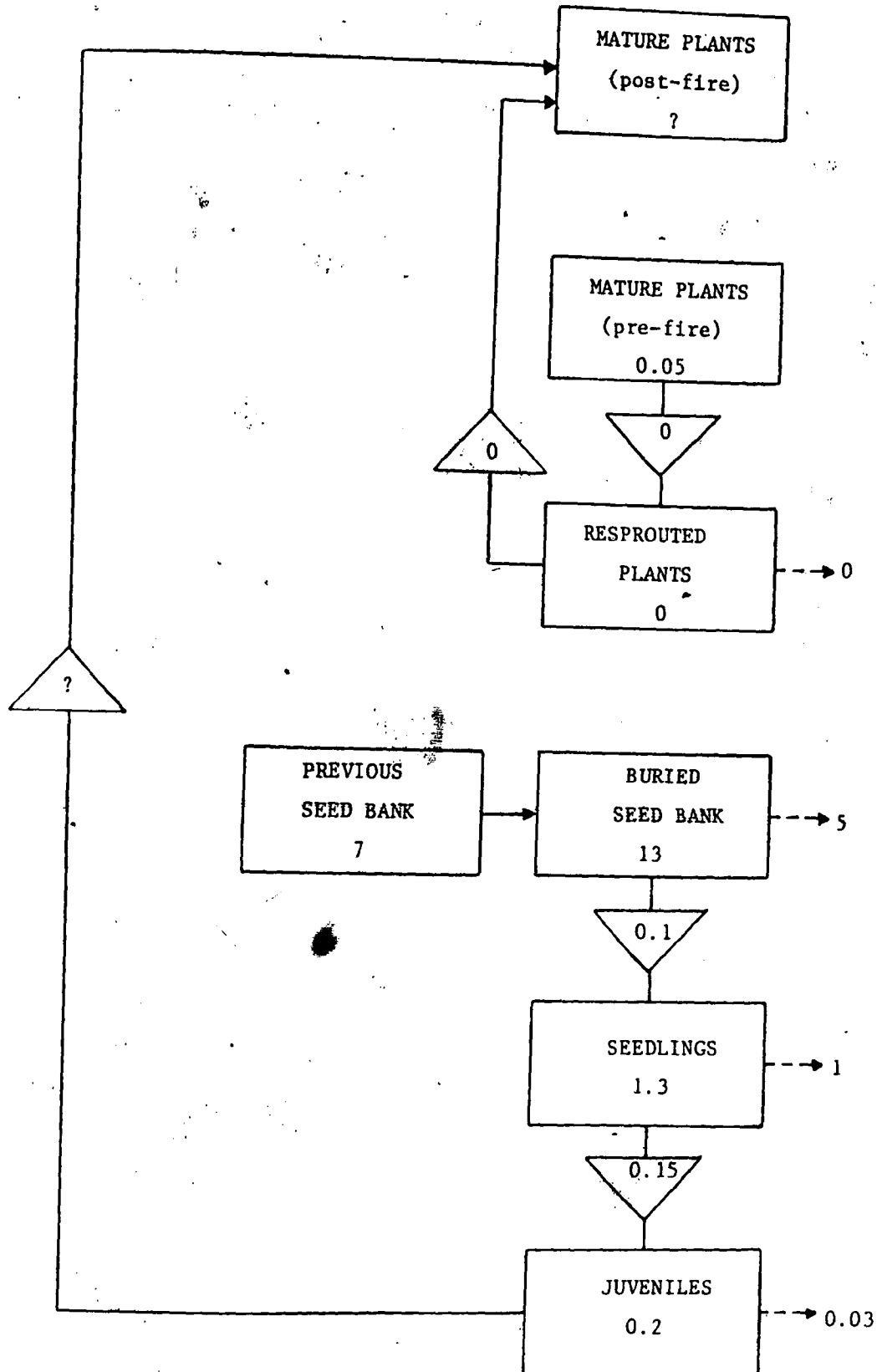lines are rounded losses from each phase.

plants arising from dormant stem buds. Since some of the juvenile plants set seed within 12 months of their emergence as well as some of the resprouts from the original mature plants, the numerical result a year after burning was similar to that in an unburnt area (Fig. 6.3). Although resprouted plants were larger in size, juveniles which matured within 12 months contributed nearly 80% to the post-fire seeding population. This would increase the chance of genetic diversity in such a population. Growth of seedlings and juveniles were much more vigorous in a burnt area (Chapter 4), which resulted in a larger percentage ground cover of these immature plants than in unburnt areas.

Fire killed all mature plants of A. longifolia but dramatically increased seed germination (Fig. 6.4).

6.1.4 Discussion

A major factor in the success of C. monilifera in Australia is apparent in the large numbers present in each of the main phases of its life table compared with the much smaller numbers of A. longifolia. For example, the greater density of seedlings of C. monilifera would tend to enhance its competitive advantage over A. longifolia (Chapter 7). Even in burnt areas, C. monilifera seedlings still outnumbered those of A. longifolia and since both species responded equally well to the greater availability of nutrients after fire (Chapter 7), the outcome of competition would be unaltered. However, insufficient time was available for estimates of seed production after fire.

In the first three interphases relating to seed production and seed rain, predation played a major part in the smaller values for A. longifolia (Chapter 3). These interphase values were much greater in South Africa (Milton & Hall 1981). Seasonal conditions are also likely to have a greater influence on the output of seeds from mature plants of A. longifolia than of C. monilifera (Chapter 3).

In the fourth interphase between the buried seed bank and seedlings, a large proportion of dormant or "hard" seeds was responsible for the lower value of A. longifolia (Chapter 4). This value would be expected to be similar in South Africa since most predation occurs of seed on the soil surface (Chapter 3).

Relative growth rates and net assimilation rates were calculated using the equations (Evans 1972):

$$RGR = (\ln w_2 - \ln w_1)/(t_2 - t_1) gg^{-1} wk^{-1}$$

where w_2 and w_1 are dry weights at times t_2 and t_1 respectively, with $t_2 - t_1 = 1$

and

$$NAR = \left[(w_2 - w_1) \ln l_2 - \ln l_1) \right]/\left[(l_2 - l_1)(t_2 - t_1) \right] g \, cm^{-2} wk^{-1}$$

where l_2 and l_1 are leaf areas at times t_2 and t_1 respectively.

Secondly, growth rates were measured in the field after an area had been control-burnt at Moruya in December 1981. Seedlings emerged in January 1982 and 32 plants of each species were marked. Seedlings were selected so that they were further than 1 m from each other and turther than 3 m from any resprouted plants and so interspecific competition was minimised. Eight plants were harvested at four times - 5, 8, 11, 15 weeks after emergence. Similar measurements to the glasshouse plants were made.

6.2.3 Results

C. monilifera had at most times a higher relative growth rate (Fig. 6.5) but its net assimilation rate was higher than A. longifolia only in older seedlings in the glasshouse (Fig. 6.6). Total leaf area, specific leaf area (leaf area per leaf dry wt.) and leaf area ratio, LAR (leaf area per total dry wt.) were all higher in C. monilifera (Table 6.1).

Total dry weight of C. monilifera was greater than that of A. longifolia only in older seedlings in the glasshouse (Fig. 6.7). In terms of percentage allocation to biomass, slightly more was invested in roots and less in stems in C. monilifera compared to A. longifolia (Fig. 6.8).

In the field, a similar picture to the glasshouse was evident in total dry weights in that C. monilifera was significantly heavier than A. longifolia only in seedlings older than 8 weeks (t-test, $P < 0.05$) (Fig. 6.9). However, root/shoot ratios were greater in A. longifolia than in C. monilifera in the field up to 11 weeks after emergence.
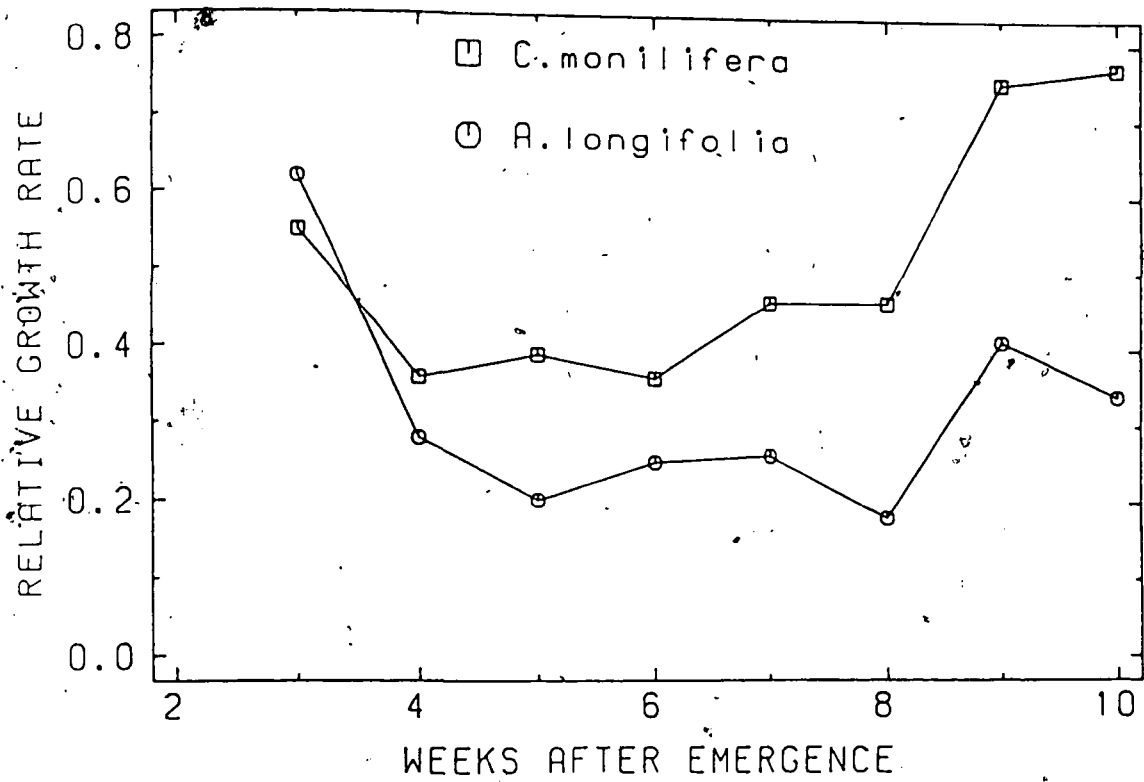
FIG. 6.5. Relative growth rates ($g\ g^{-1}\ wk^{-1}$) of <u>C. monilifera</u> and <u>A. longifolia</u> seedlings in the glasshouse.
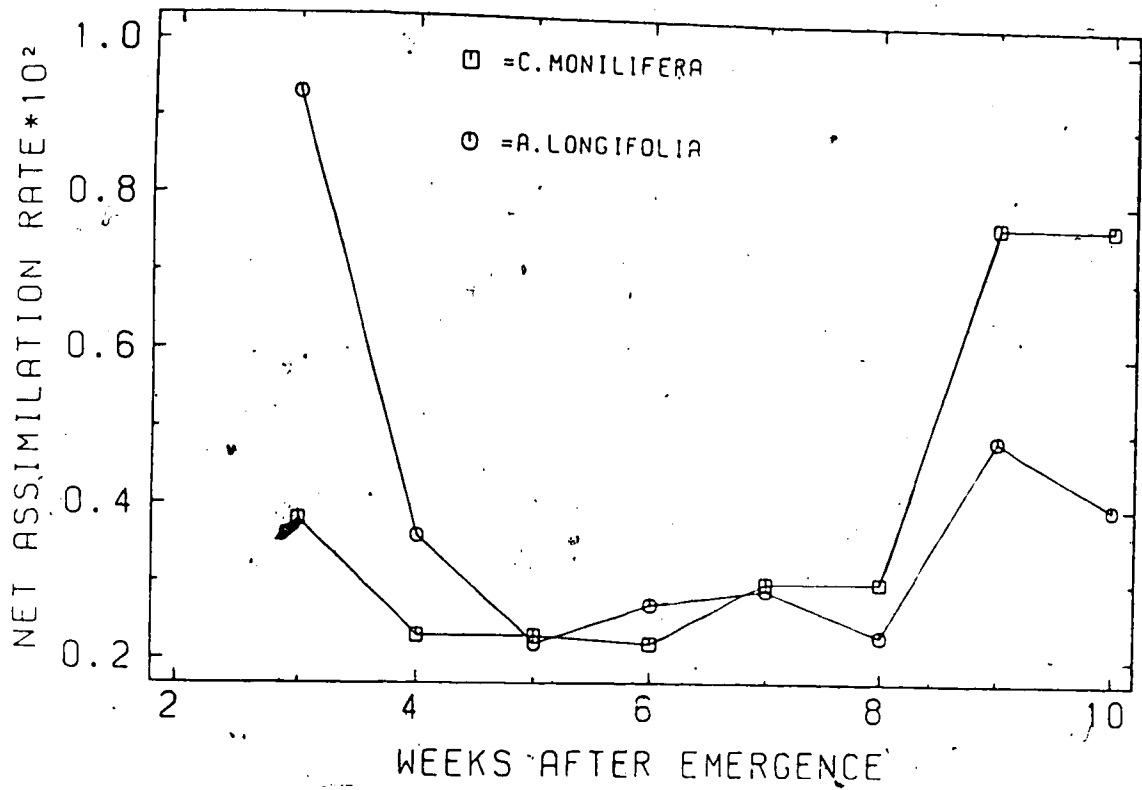
FIG. 6.6. Net assimilation rates (g cm^{-2} wk^{-1}) of <u>C. monilifera</u> and <u>A. longifolia</u> seedlings in the glasshouse.
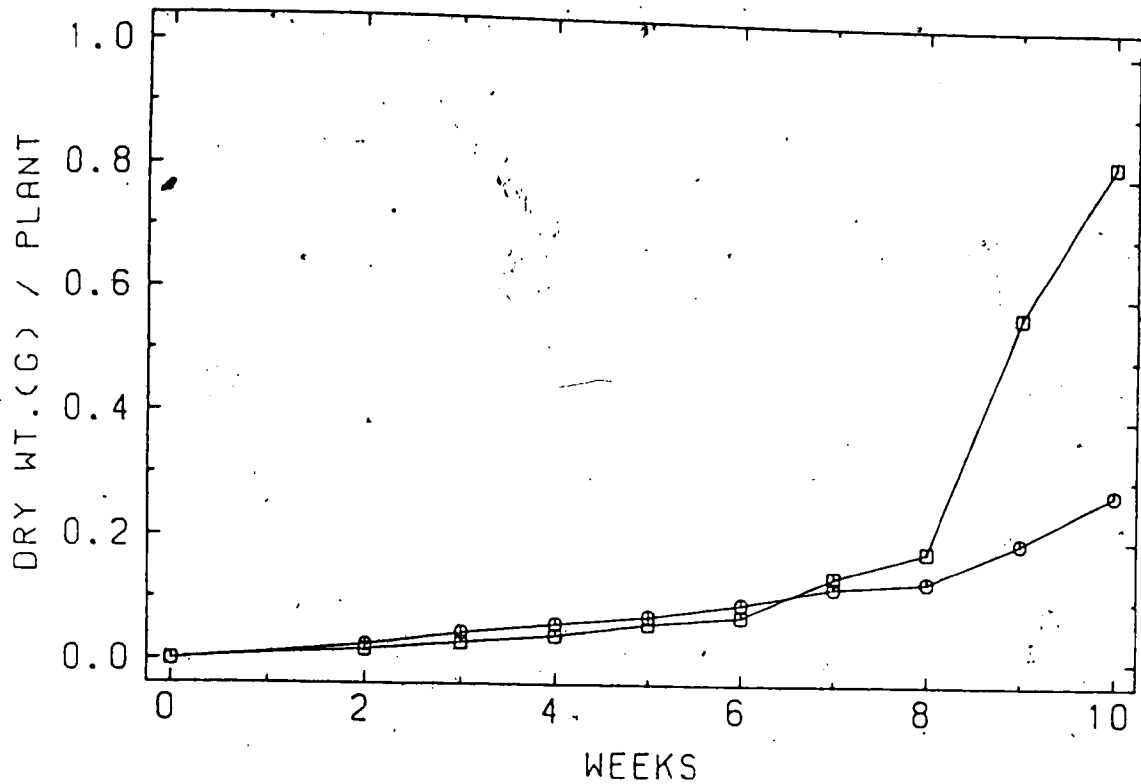
FIG. 6.7. Total dry weights per plant of C. monilifera (□) and
A. longifolia (O) harvested at various times after
emergence in the glasshouse.
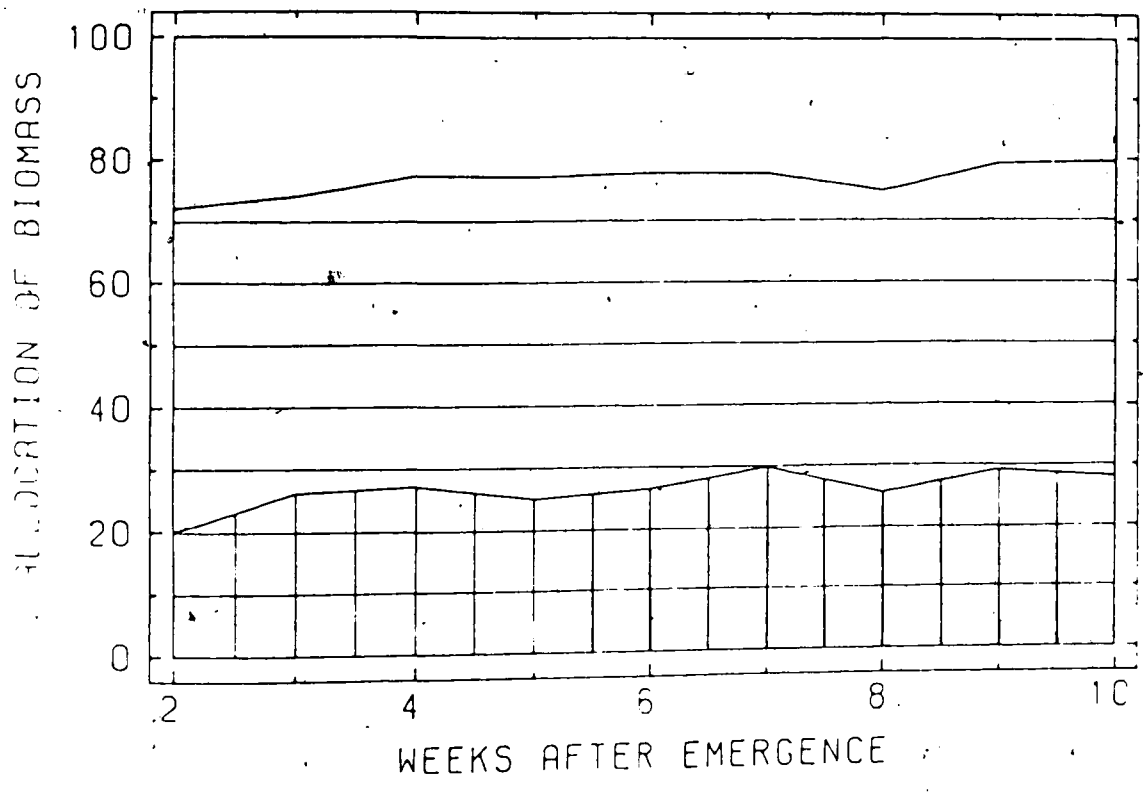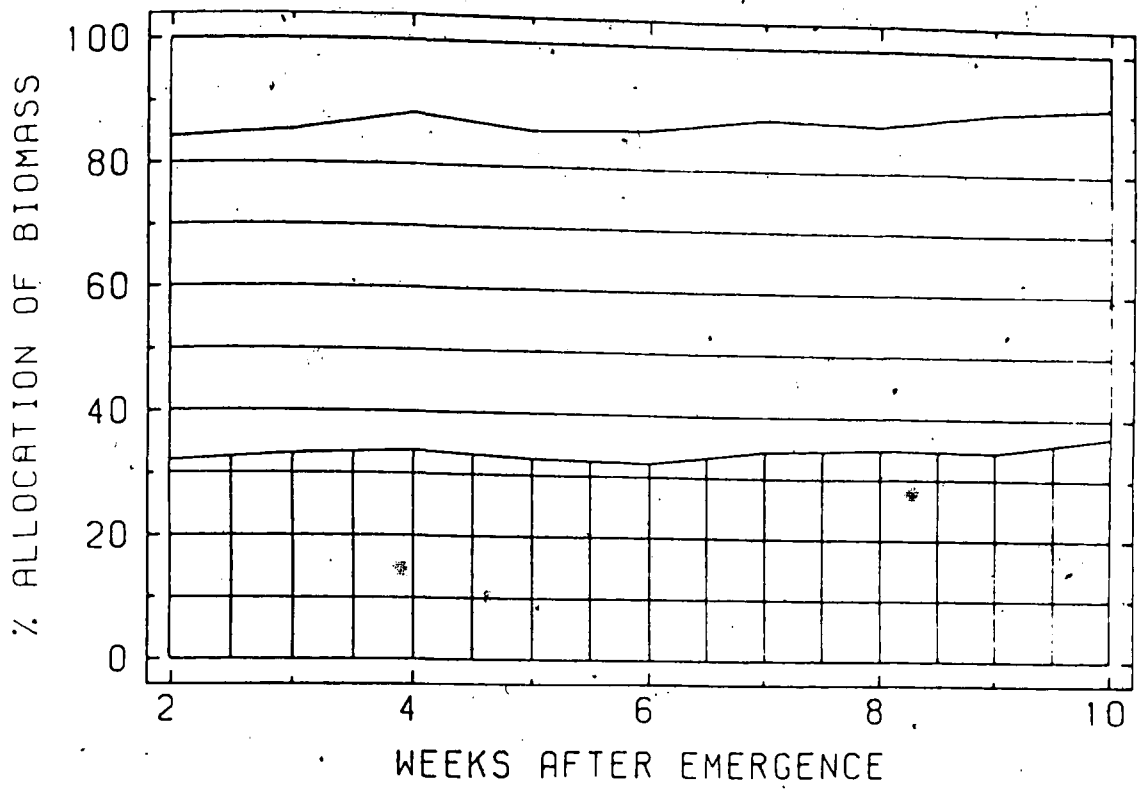
FIG. 6.8. Allocation of biomass into roots (⊞), leaves (⊟) and
stems (☐) in seedlings of C. monilifera (top) and
A. longifolia (bottom) at various times after emergence
in the glasshouse.
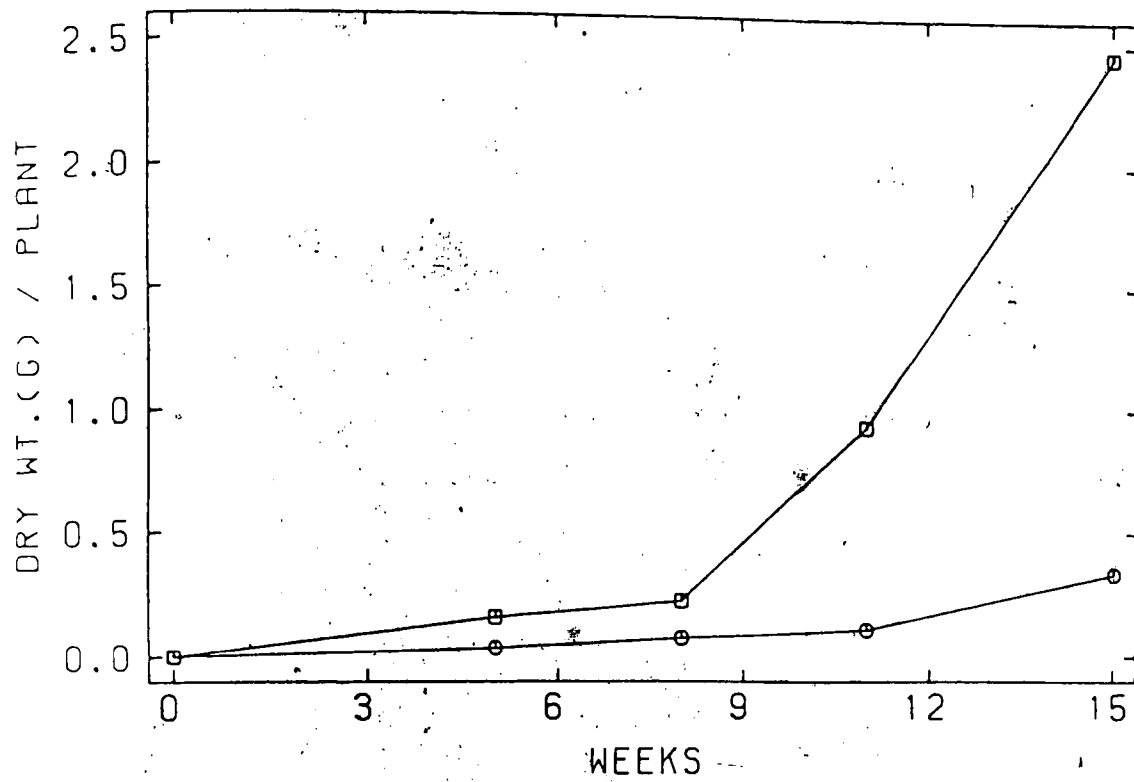
FIG. 6.9. Total dry weights per plant of C. monilifera (□)
and A. longifolia (O) harvested at various times after
emergence in the field.

FIG. 6.10. Two seedlings of <u>A. longifolia</u> (top), showing
Bipinnate leaves, 4 weeks after emergence and three
of <u>C. monilifera</u> (bottom) 8 weeks after emergence
in a mid-dune area at Moruya burnt in December 1981.
Scale is 1 cm to 1.12 cm.

Table 6.1   Total leaf area, specific leaf area and leaf area ratio of
C. monilifera (C) and _A. longifolia_ (A) seedlings at weekly
intervals in the glasshouse.   Standard errors are given in
parentheses

Time after emergence (weeks)	Leaf area (cm^2)		Specific leaf area (cm^2 g^{-1})		Leaf area ratio (cm^2 g^{-1})	
	C	A	C	A	C	A
2	2.4(0.2)	1.4(0.2)	284 (24)	106 (3)	148 (16)	55 (7)
3	4.2(1.2)	3.4(0.3)	267 (36)	157 (4)	143 (18)	75 (3)
4	6.5(1.1)	4.8(0.3)	290 (10)	163 (8)	157 (14)	82 (4)
5	10.3(2.4)	6.8(0.7)	273 (10)	179 (9)	145 (12)	93 (6)
6	11.8(2.1)	8.9(0.5)	307 (21)	186 (4)	168 (15)	96 (3)
7	20.5(8.7)	10.1(0.7)	257 (22)	164 (3)	144 (18)	78 (2)
8	24.2(6.5)	11.0(1.3)	253 (15)	193 (5)	134 (11)	95 (1)
9	65.7(4.9)	16.7(1.8)	210 (13)	173 (7)	116 (4)	86 (3)
10	72.4(8.1)	23.9(2.2)	194 (7)	168 (5)	113 (5)	86 (2)

Table 6.2 Root weights per plant and root/shoot ratios of C. monilifera (C) and A. longifolia (A) up to 15 weeks after emergence in the field. Standard errors are given in parentheses

Time after emergence (weeks)	Roots (g plant^{-1})		Root/Shoot (g/g)	
	C	A	C	A
5	0.02 (0.005)	0.01 (0.001)	0.12 (0.01)	0.35 (0.05)
8	0.02 (0.004)	0.01 (0.003)	0.08 (0.01)	0.14 (0.03)
11	0.10 (0.02)	0.02 (0.004)	0.13 (0.02)	0.23 (0.05)
15	0.41 (0.12)	0.05 (0.01)	0.20 (0.01)	0.20 (0.01)

This position was reversed when only root weights were considered (Table 6.2).

Although only plants at the same age were compared in the field, most seedlings of C. monilifera emerged before those of A. longifolia (Fig. 6.10). Thus it was usual to find seedlings of C. monilifera more advanced than those of A. longifolia.

6.2.4 Discussion

It is apparent that C. monilifera has a number of advantages over A. longifolia in the seedling stage which would be of benefit in a competitive situation and help explain the outcome of the interactions investigated in Chapter 7. These are:

1. A higher relative growth rate. Since C. monilifera has a higher leaf area ratio, this would tend to offset any lower photosynthetic rate per unit leaf area (Chapter 8) and could well lead to the higher relative growth rate observed in this species since:

$$RGR = NAR \times LAR = \frac{dw}{dt} \cdot \frac{1}{l} \times \frac{l}{w} \quad \text{(Evans 1972)}$$

$$= \frac{dw}{dt} \cdot \frac{1}{w}$$

where l represents leaf area and w total plant weight.

2. Earlier emergence in the field than A. longifolia especially if comparatively dry conditions are present, as was predicted from laboratory experiments (Chapter 4).

3. The larger leaf area of C. monilifera would lead to shading of A. longifolia where the two were growing in close proximity, as frequently occurs in the field (Fig. 6.10).

4. The higher root weights of C. monilifera which were also more extensive in the soil would be advantageous in obtaining more soil moisture.

6.3 Shoot growth.

6.3.1 Introduction

When seedlings have reached the "established" phase, their success is still at least partly determined by seasonal timing of shoot growth as well as the extent of that growth. Earlier and more extensive shoot production would be likely to place one species at a competitive advantage over another especially if they were growing in close proximity.

The shoot growth of the invasive species, Pinus radiata, has been compared by Foster (1979) with that of Eucalyptus sp. in invaded forests in Australia. He found that both species had maximum growth at the same time of the year but P. radiata started growing earlier in spring as soon as water became plentiful. In South Africa, Milton & Moll (1982) attributed part of the invasive ability of A. longifolia to rapid shoot growth in the spring and summer. In order to establish if a similar pattern existed with C. monilifera and A. longifolia in Australia, I followed the shoot production of mature plants in the field over a 12 month period.

6.3.2 Methods

An estimate of the seasonality of shoot growth was obtained by measuring elongation of all shoots on 20 mature plants of each species in unburnt areas at Moruya. Ten plants of A. longifolia were located in an area invaded by C. monilifera and ten in an uninvaded area. Measurements were made at 4 to 8 weekly intervals between March 1981 and March 1982.

6.3.3 Results

Both species showed a similar pattern in shoot elongation during the year although C. monilifera increased slightly more than A. longifolia between winter and spring (Fig. 6.11). However, five plants of A. longifolia (three in the invaded area and two in the uninvaded area) had a large proportion of their stems die during the period of measurement due to presence of insects (Chrysolofus sp. and Uracanthus sp.) which were found inside the stems. These plants were not included in deriving the mean values presented.
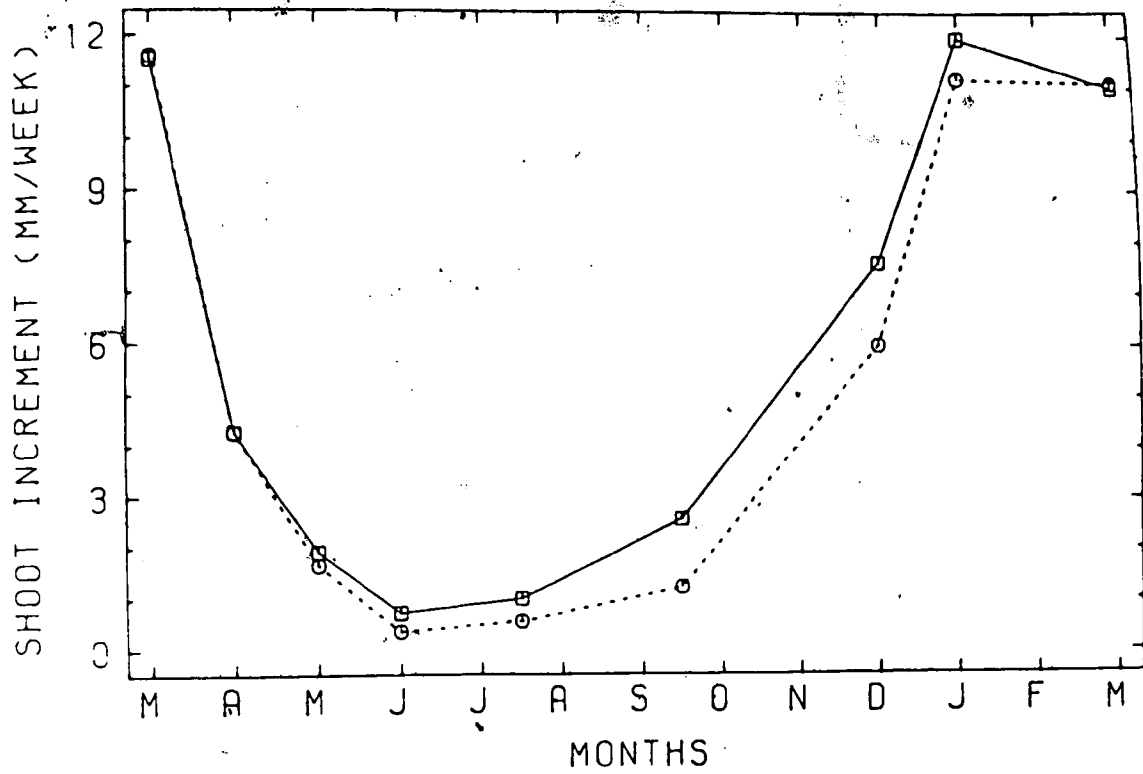
FIG. 6.11. Rates of growth of shoots, expressed as mm wk^{-1}, of mature plants of C. monilifera (□) and A. longifolia (O) in the field at Moruya.

Shoot growth of both species slowed in winter but most shoots of C. monilifera diverted growth from leaf and stem production to flowers and seeds at this time (Chapter 3).

6.3.4 Discussion

Differences between C. monilifera and A. longifolia in the seasonality of shoot growth were not sufficiently different to explain the invasive ability of C. monilifera. However, the fact that the results in the two species are numerically similar is not very critical since leaf production was not measured. In addition, plasticity in growth form may be more important than the amount of shoot growth. Thus in some situations, e.g. where C. monilifera was growing next to a taller species such as B. integrifolia, the normally prostrate growth form of C. monilifera became more of an upright one because of support for its stems and so it was able to "smother" other taller species.

The phase of growth (whether vegetative or reproductive) would also seem to be important in invasive ability; growth of C. monilifera was often channelled into reproduction which covered a much longer period of the year than A. longifolia (Chapter 3). However, this would tend to place C. monilifera at a disadvantage if growing with A. longifolia. On the other hand, terminal shoot growth of A. longifolia often became necrotic which would offset any advantage.

6.4 Summary

The advantage of C. monilifera in terms of numbers at different stages in the life table was apparent and is a major factor in accounting for the success of C. monilifera in Australia (Table 6.3). Most of the inferences made from data in other chapters on the two species being studied was borne out by their seedling behaviour in the field. Thus C. monilifera had superior growth to A. longifolia especially when seedlings became established. However, the studies reported in this chapter were made on isolated plants and competition may affect the outcome. This led to an investigation of competitive effects when plants were in close proximity which is reported in the next chapter.

Table 6.3 Summary of seedling growth, shoot growth of mature plants
and life table characteristics of C. monilifera (C) and A.
longifolia (A)

Attribute	Comparison
Relative growth rate (seedlings)	Higher in C than A.
Net assimilation rate, total dry weight (seedlings)	Higher in C than A only after 8 weeks.
Root/shoot weight (seedlings)	Higher in A than C up to 11 weeks after emergence in the field.
Total leaf area, specific leaf area, leaf area ratio (seedlings)	Higher in C than A.
Shoot production (mature plants)	Peak occurs in late summer. Slightly earlier winter-spring growth occurs in C than A. Terminal growth of A is often necrotic.
Seed production, seed bank, densities of seedlings and juveniles	Higher in C than A.
Interphases between seed production and seed bank	Lower in A than C because of predation.
Interphase between seed bank and seedlings	Low in C and is somewhat reduced by fire. Very low in A and greatly increased by fire.

Chapter 7

Interactions between Chrysanthemoides and Acacia

"Where there is so much of competition and uncertainty you must expect
self interest will govern."
(Collier 1697)

"The outcome of competition between cluster pine and acacias and the
indigenous flora will be an impoverishment of species, resulting in a
vegetation of monotonous and mournful character."
(Bolus & Wolley-Dod 1904)

"... all the plants of a given place are in a state of war with
respect to each other."
(De Candolle 1820)

Introduction

The importance of studying interactions between plants has been succinctly set out by Harper (1964): "The essential qualities which determine the ecology of a species may only be detected by studying the reaction of its individuals to their neighbours and the behaviour of individuals of the species in isolation may be largely irrelevant to understanding their behaviour in the community."

The experiments reported here examined interactions between C. monilifera and A. longifolia in order to quantify such interactions and to examine the factors involved, which may help explain their behaviour in coastal communities. Some of these factors in plant interactions in general were enumerated by Clements, Weaver & Hanson (1929). They considered the following points in the life form of a plant largely determined its competitive ability:

(a) Duration or perennation;

(b) Rate of growth particularly as expressed by expansion and density of shoots and roots;

(c) Rate and amount of germination; and

(d) Vigour and hardiness which facilitate survival under stress.

Rate of growth of C. monilifera, particularly of seedlings was greater than that of A. longifolia (Chapter 6). Similarly, the rate and amount of germination of C. monilifera was greater than that of A. longifolia (Chapter 4). I decided to study (d) above, particularly in relation to the effect of water stress on competition, since soil water content in the field is often low (Chapter 9). I also investigated the relative effects of root and shoot competition and seed production of A. longifolia as affected by competition from C. monilifera.

C. monilifera may also be successful because of an allelopathic effect on A. longifolia so I tested leachates from C. monilifera on seed germination of A. longifolia under controlled conditions. I also sowed seeds of each species at varying distances from mature plants of both species in the field, although allelopathic, competitive and environmental effects were not separated in this experiment.

7.1 Water stress

7.1.1 Introduction

A general principle concerning the role of the relationships of water in plant competition has been enunciated by Milthorpe (1961): the greater a plant's leaf growth before it comes into contact with another plant, the more extensive will be its root system and the less it is likely to suffer from drought. Two specific examples show that water may have different effects on competition, depending on the importance of water in the natural habitat of the plants. Thus Erica cinerea (heath), a plant of dry soils, is outcompeted by Calluna vulgaris (heather), characteristic of moist soils, when grown in moist soils in the laboratory. However, the position is reversed when these species are grown together in dry soil (Bannister 1976). On the other hand, Pearcy, Tumosa & Williams (1981) found that limiting the water supply had no effect on the competitive interactions between the weeds Chenopodium album (fat-hen) and Amaranthus retroflexus (amaranth). This may have been because these species commonly grow in the same habitat, unlike the heath species cited above.

The aim of the experiments conducted on C. monilifera and A. longifolia was to investigate the effect of water stress on the outcome of competition. Stress was applied by three methods under glasshouse conditions:

1. withholding water for fixed intervals up to 12 days but in each treatment giving the same total amount of water over the period of the experiment;

2. withholding water for fixed intervals and watering each time to approximately field capacity; and

3. withholding water until plants wilted and then watering to approximately field capacity.

Chlorophyll concentration was measured in one experiment to determine if it was affected by competition and/or water stress since rate of photosynthesis is proportional to chlorophyll content (eg. Baker & Hardwick 1976). Carbohydrates were also measured in another experiment as a further check on photosynthetic activity since

they reflect the carbon balance of the plant (gross photosynthesis minus respiration).

7.1.2 Methods

Three experiments were conducted using the standard method of the replacement series of de Wit (1960) in which the two species are grown together at the same overall density but in varying proportions (Table 7.1). Unsterilised sand-dune soil from Moruya was used in all experiments (previous tests had shown that both species were equally stimulated in steam-sterilised soil). In this and the following section, day/night temperatures in the glasshouse were 25/15°C, with natural lighting.

The "tube" experiment was designed to examine root growth and after harvesting the roots were washed gently in running water and separated. At the first harvest, but not the second when roots in all treatments had reached the bottom of the tubes, roots were then cut into 10 cm sections. After drying at 80°C and weighing, the root sections from the first harvest were bulked and roots and shoots ground separately in a hammer mill. Approximately 10 mg of ground material was used in a glucose specific assay, using an enzymatic method of S.C. Wong (Appendix 1). Starch was analysed using a similar enzymatic method which hydrolyzed starch and sucrose to hexoses.

In the "wilt" experiment, leaf chlorophyll was measured on the whole of the second fully expanded leaf from the top of a plant. Leaf area and specific leaf weight were obtained and the leaf then ground in 80% acetone. The samples were centrifuged for 5 min and the absorbance of each read on a spectrophotometer at a range of wavelengths, with a solution of 80% acetone as a standard. The readings at 645, 663 and 710 nm were used in the determination of chlorophyll a and b (Arnon 1949).

7.1.3 Results
7.1.3.1 "Tube" experiment

C. monilifera emerged 2 to 3 days earlier than A. longifolia and biomass of C. monilifera was consistently greater than that of A. longifolia except in monocultures after 5 months. However, competitive effects were not pronounced until the second harvest (Figs. 7.1, 7.2, 7.3). At that stage, the non-linearity of the replacement curves shows the extent that C. monilifera outcompeted A. longifolia. Water stress (6 and 12 day watering) minimised the

Table 7.1 Summary of glasshouse experiments on the effect of water stress on competition between C. monilifera and A. longifolia seedlings. Pre-germinated seeds were cut at the distal end and germinated in petri dishes before sowing

Exp.	Pots	Seeds	Proportions of each species	Density /pot	Time between watering	Duration	Measurements
"Tube"	10.5 cm diam. tubes, 60 cm long	Not germinated before sowing	0, 0.5, 1	4	0 (sub-irrigation), 1,6,12 days	Harvests at 2 and 5 months after emergence	Carbohydrates at first harvest. Root, leaf and stem dry weights at both harvests.
"Time"	15 cm diam. pots	Pre-germinated	0, 0.5, 1	8	3,6,12,15, 18 days	2 months after emergence	Numbers of surviving plants every 3 days.
"Wilt"	15 cm diam. pots	Pre-germinated	0, 0.2, 0.3, 0.5, 0.7, 0.8, 1.0	6	1 day or until wilting	2 months after emergence	Leaf chlorophyll. Stem length, leaf number, area. Root, stem and leaf dry weights.

Table 7.2 Root and shoot weights per plant of C. monilifera and A. longifolia 2 and 5 months after emergence in monocultures and a 1:1 mixture in the "tube" experiment. Values are averages of the 0 and 1 day watering treatment (no stress) and of the 6 and 12 day treatment (stress)

Species	No water stress			Water stress		
	Roots (g)	Shoots (g)	Root/ Shoot	Roots (g)	Shoots (g)	Root/ Shoot
Monoculture			2 months			
C. monilifera	0.07	0.12	0.58	0.08	0.06	1.33
A. longifolia	0.02	0.04	0.53	0.02	0.03	0.67
Mixture						
C. monilifera	0.11	0.07	1.52	0.09	0.07	1.24
A. longifolia	0.02	0.02	0.90	0.02	0.02	1.22
Monoculture			5 months			
C. monilifera	0.90	0.52	1.73	0.74	0.45	1.65
A. longifolia	0.64	0.95	0.68	0.39	0.52	0.75
Mixture						
C. monilifera	1.61	0.87	1.85	1.05	0.60	1.76
A. longifolia	0.13	0.26	0.49	0.09	0.13	0.68

Table 7.3 Concentrations of glucose and starch 2 months after emergence of C. monilifera and A. longifolia under four watering regimes in the glasshouse. Standard errors are in parentheses

Time between watering (days)	C. monilifera		A. longifolia	
	Shoots	Roots	Shoots	Roots
	mg glucose/mg dry wt.			
0	0.029 (0.008)	0.015 (0.005)	0.030 (0.003)	0.007 (0.001)
1	0.027 (0.005)	0.016 (0.006)	0.048 (0.006)	0.007 (0.003)
6	0.031 (0.008)	0.011 (0.003)	0.053 (0.010)	0.012 (0.003)
12	0.021 (0.002)	0.011 (0.003)	0.037 (0.007)	0.006 (0.002)
	mg starch/mg dry wt.			
0	0.024 (0.010)	0.018 (0.005)	0.124 (0.024)	0.034 (0.011)
1	0.025 (0.007)	0.021 (0.003)	0.102 (0.018)	0.024 (0.004)
6	0.020 (0.004)	0.017 (0.003)	0.100 (0.011)	0.024 (0.007)
12	0.026 (0.003)	0.018 (0.008)	0.110 (0.023)	0.028 (0.006)

Table 7.4 Area of leaf samples of C. monilifera (C) and A. longifolia (A) in a replacement series with a total density of six plants per pot under two watering regimes. Standard errors are in parentheses

| No. of plants in mixture | | Area/leaf (cm^2) | | | |
| | | C. monilifera | | A. longifolia | |
C	A	Water stress	No stress	Water stress	No stress
0	6	–	–	2.6 (0.4)	7.3 (1.6)
1	5	5.0 (1.1)	8.9 (1.9)	2.6 (0.5)	7.9 (1.5)
2	4	4.8 (1.0)	7.8 (1.7)	2.9 (0.6)	5.8 (1.1)
3	3	2.2 (0.8)	7.3 (1.7)	2.3 (0.4)	3.6 (0.7)
4	2	2.9 (0.7)	5.9 (1.5)	2.7 (0.5)	3.7 (0.8)
5	1	1.8 (0.4)	4.7 (1.0)	2.6 (0.5)	2.1 (0.4)
6	0	1.7 (0.4)	4.7 (1.1)	–	–
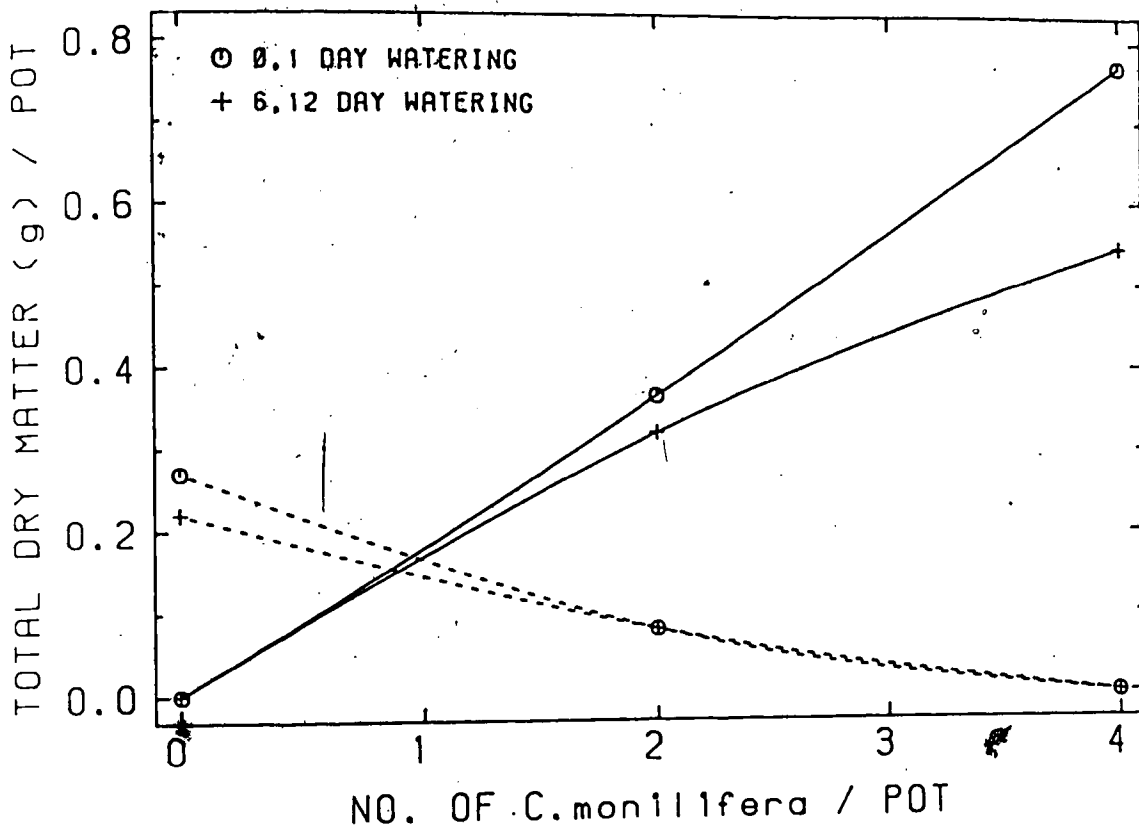
FIG. 7.1. Total dry matter weights per pot of C. monilifera
(solid line) and A. longifolia (dashed line) in a
monoculture and 1:1 mixture, with a total of four plants
per pot, 2 months after emergence, under water stress
and no stress.
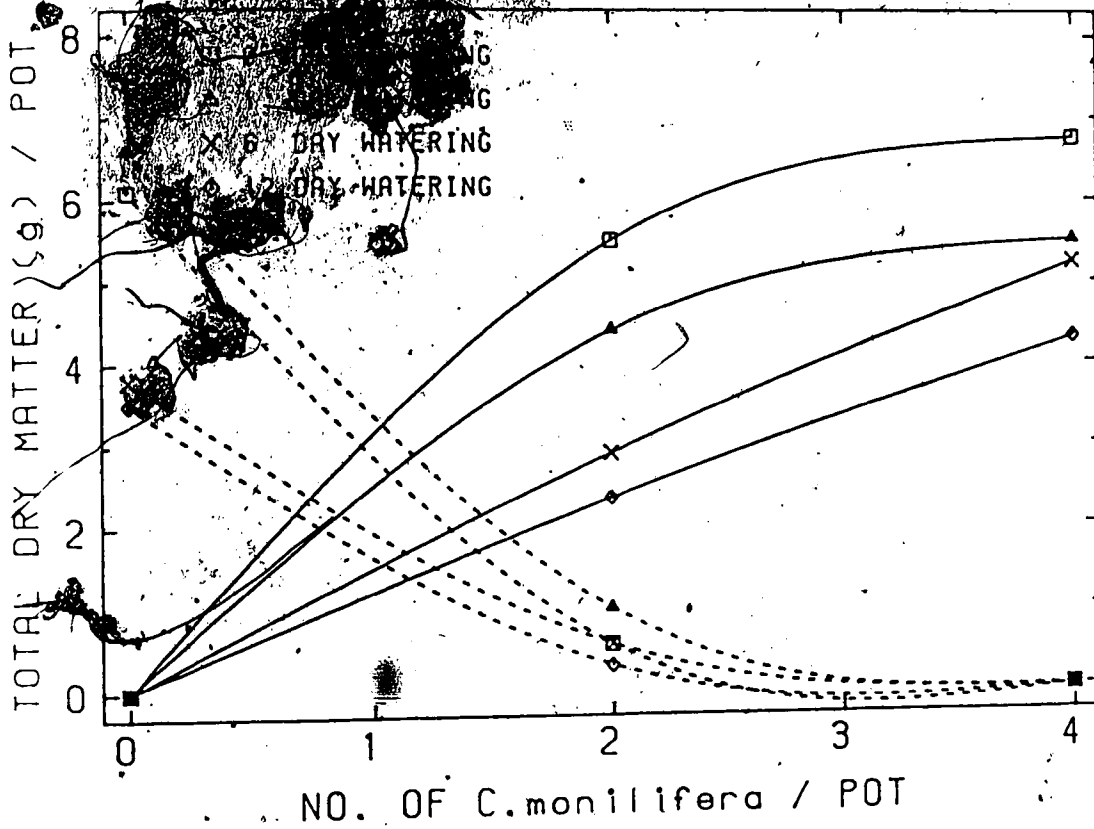
FIG. 7.2. Total dry matter weights per pot of C. monilifera
(solid line) and A. longifolia (dashed line) in a
monoculture, and 1:1 mixture, with a total of four
plants per pot, 5 months after emergence, under four
watering regimes.

FIG. 7.3. Growth of monocultures with daily watering of <u>C. monilifera</u> ssp. <u>rotundata</u> (middle) and <u>A. longifolia</u> var. <u>sophorae</u> (right) and a 1:1 mixture of the two species (left) in the 'tube' experiment.
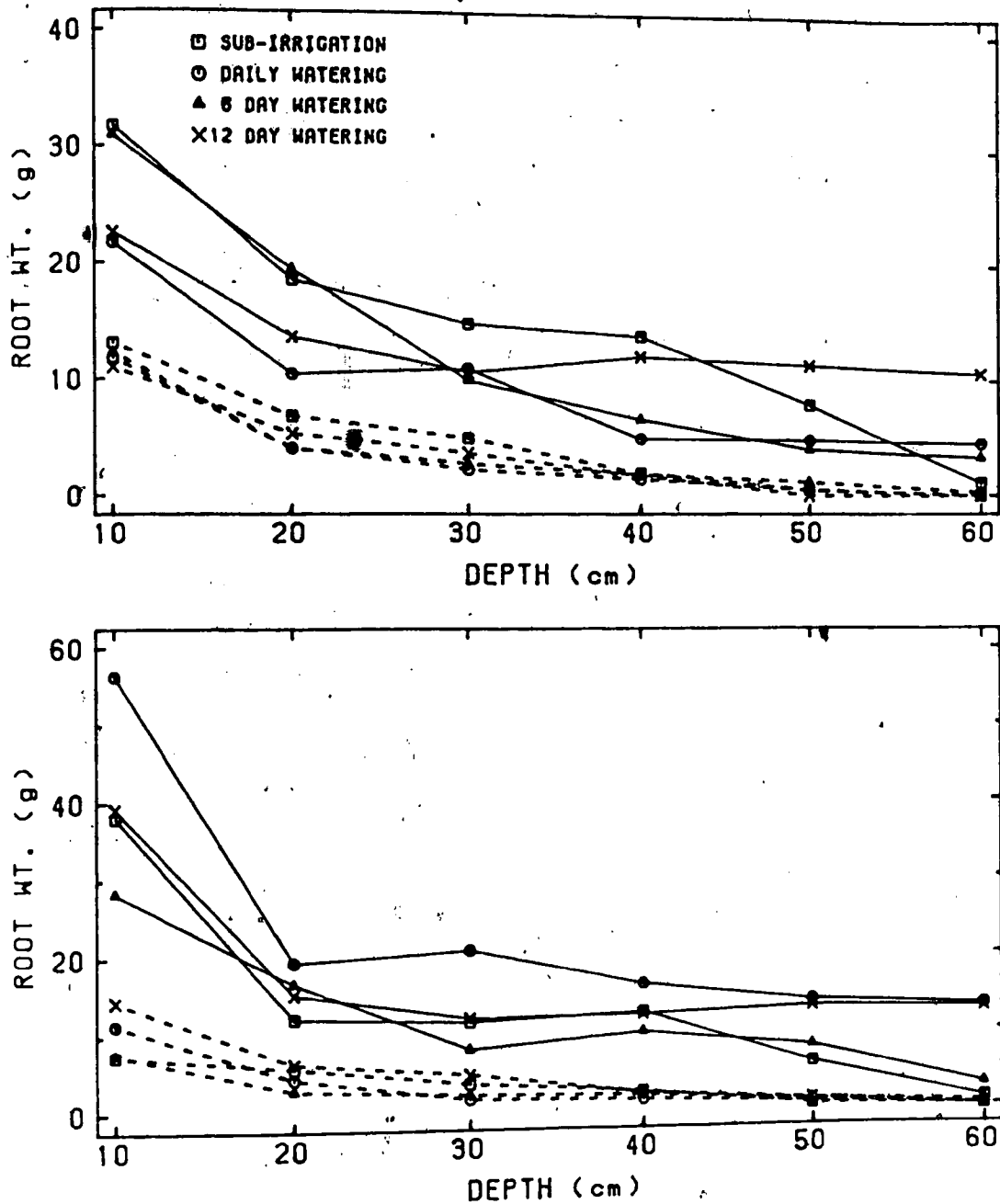
FIG. 7.4.   Root weights per plant 2 months after emergence at soil
            depths of 0-10, 10-20, 20-30, 30-40, 40-50, 50-60 cm
            under four watering regimes in monocultures (top) and
            1:1 mixture (bottom) of C. monilifera (solid line)
            and A. longifolia (dashed line).
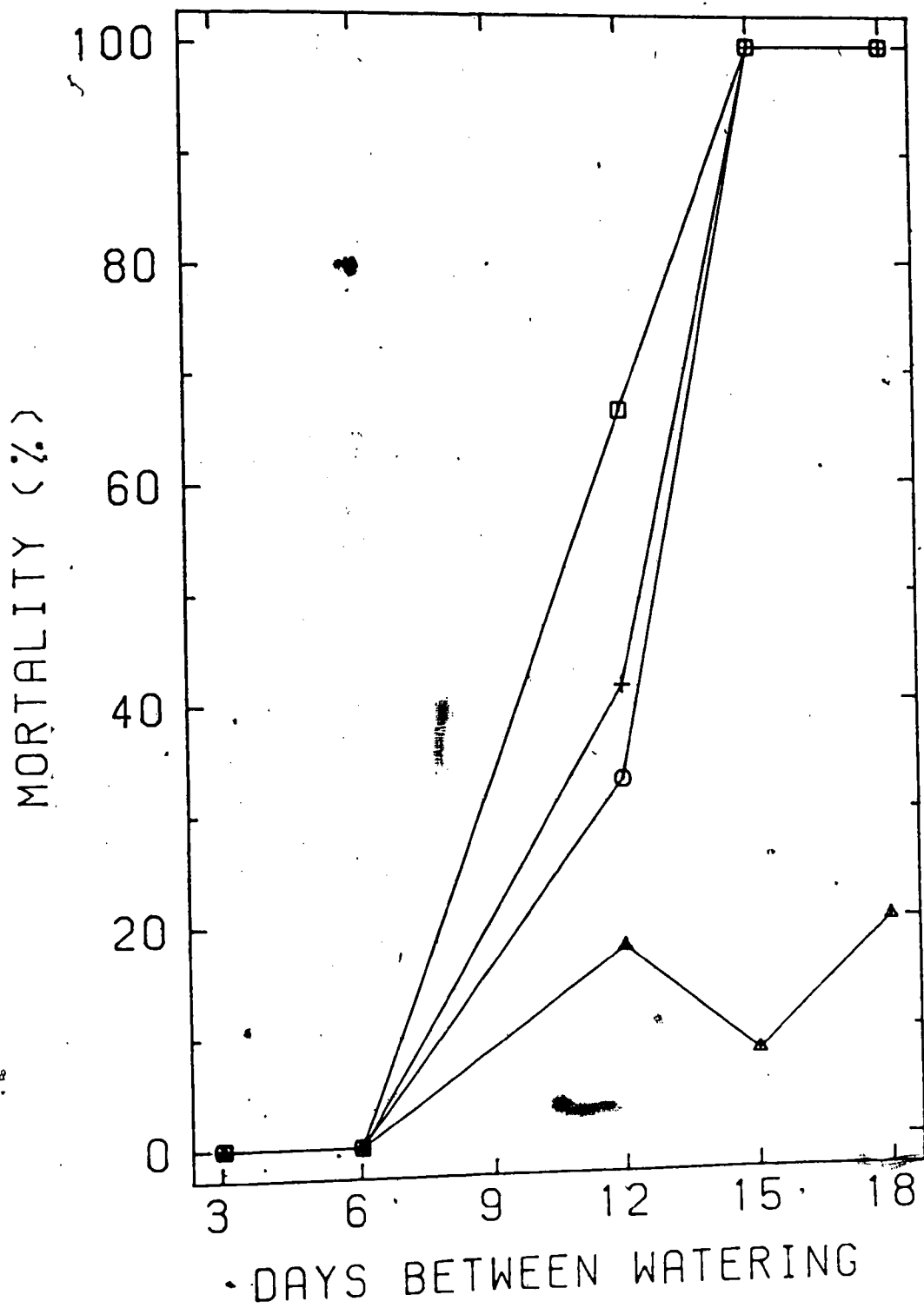
FIG. 7.5. Mean percentage mortalities of C. monilifera in
monoculture (□) and in a 1:1 mixture (+) and
A. longifolia in monoculture (Δ) and in a 1:1
mixture (0), under five watering regimes, 2 months
after emergence.

competitive advantage of C. monilifera over A. longifolia. There were no significant differences in total dry matter weight in either species between the 6 and 12 day watering regimes or between those of sub-irrigation and daily watering (ANOVA, P > 0.05).

In both species most of the roots were in the top 10 cm of soil but C. monilifera had both a greater total weight and a greater penetration of roots than A. longifolia (Fig. 7.4). The root/shoot ratio was also higher in C. monilifera in all treatments (Table 7.2). Only A. longifolia showed consistent increases in the root/shoot ratio with water stress. The ratio increased in C. monilifera between 2 and 5 month old plants but did so in A. longifolia only in monocultures.

The results for the carbohydrate analyses have been pooled for monocultures and mixtures since there were no significant differences between them (t-test, P > 0.05). Averaged over all watering treatments, A. longifolia had one and a half times more soluble sugar in the form of glucose per unit dry·weight of shoots than C. monilifera (Table 7.3). A. longifolia also had four times more starch per unit dry weight of shoots than C. monilifera.

7.1.3.2 "Time" experiment

Unlike the previous experiment, some plant mortality· occurred with a 12 day watering interval because of a smaller soil volume. Mortality was comparatively low in monocultures of A. longifolia (even with an 48 day watering interval) and high in monocultures of C. monilifera, while that of C. monilifera decreased and of A. longifolia increased in a mixture of the two species (Fig. 7.5).,

7.1.3.3 "Wilt" experiment

When watered daily, A. longifolia in monocultures grew in its normal prostrate form but stress in the form of withholding water or competition with C. monilifera caused a markedly upright habit of growth and a trend towards shorter stems.

The sampled leaf area (ie. of the second fully expanded leaf) of C. monilifera decreased with increasing density of this species in mixtures under both watering regimes (Table 7.4). With A. longifolia, leaf area was similar between plant densities in the water stress treatment although when watered daily, leaf area declined with decreasing density (and increasing competition with C. monilifera).

The results for the chlorophyll analyses have been pooled for the two watering regimes since there were no significant differences in either species (t-test, $P > 0.05$). Chlorophyll concentration per unit leaf area was significantly greater in monocultures of A. longifolia compared to those of C. monilifera or compared to levels in A. longifolia where there were four or less plants of this species in a mixture (Table 7.5). There were no significant differences in C. monilifera between densities.

In the water stress treatment, the total dry matter data fitted most closely a "mutual depression" model (de Wit 1960), in which the total yield of the mixture was lower than that of the monocultures, (Fig. 7.6). However, a curve was not fitted because of the discrepancy in the values for C. monilifera in monoculture. These low values were due to the monoculture exhibiting the severest wilting each time before watering, leading to death of a large number of leaves.

There was a more marked interaction between the two species in the daily watering treatment (Fig. 7.7) and here the best model (de Wit 1960) was a replacement of A. longifolia by C. monilifera with $k_{ca} = 1/k_{ac}$, where k_{ca} is the crowding coefficient of C. monilifera with respect to A. longifolia, which was fitted for both total biomass and root weight in Fig. 7.7. In the case of total weight, $k_{ca} = 4.79$ and $k_{ac} = 0.21$, which indicates the extent of the competitive advantage of C. monilifera over A. longifolia. There was little difference between the two species in monocultures in total dry weight but there was a markedly higher root weight in C. monilifera (Fig. 7.7).

7.1.4 Discussion

The greater root development in C. monilifera compared to A. longifolia, evident in the "tube" and "wilt" experiments, would be advantageous in the field in obtaining the often limited supply of water in coastal sand dunes (Chapter 9).

The higher chlorophyll concentrations found in shoots of A. longifolia are probably responsible for its higher rate of assimilation per unit leaf area in the glasshouse (Chapter 8), which in turn would lead to the greater carbohydrate concentrations found. However, the greater total leaf area of C. monilifera (Chapter 6), especially in the early stages of growth when A. longifolia has bipinnate leaves before phyllodes are developed, enables it to outgrow

Table 7.5 Total chlorophyll concentrations of $\underline{C}$. $\underline{monilifera}$ (C) and
$\underline{A}$. $\underline{longifolia}$ (A) in a replacement series with a total
density of six plants per pot. Values are means under two
watering regimes. Standard errors are in parentheses

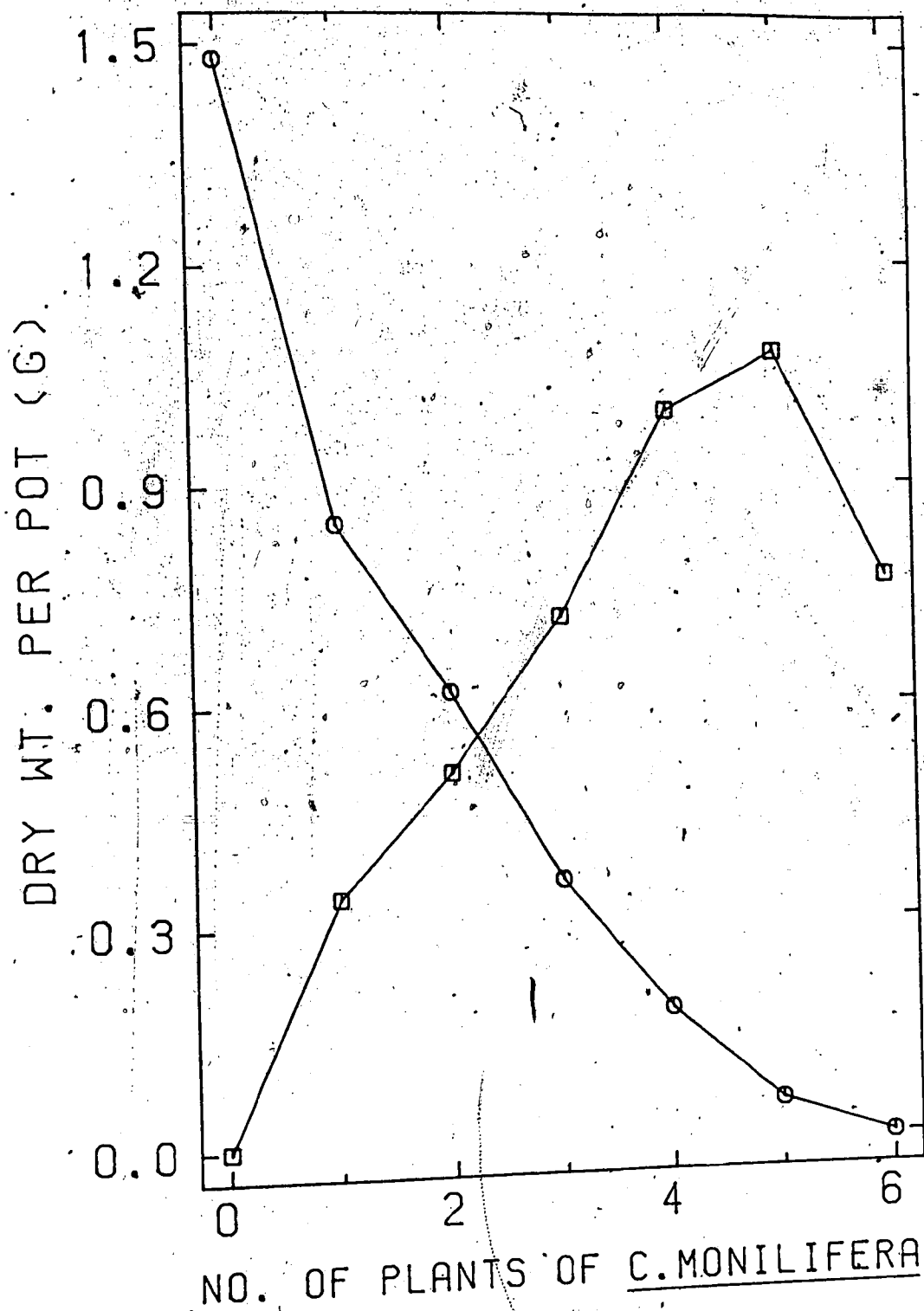| No. of plants in mixture | | $\underline{C}$. $\underline{monilifera}$ $g\ m^{-2}$ | $\underline{A}$. $\underline{longifolia}$ $g\ m^{-2}$ |
C	A		
0	6	–	0.67 (0.02)
1	5	0.32 (0.07)	0.55 (0.09)
2	4	0.40 (0.09)	0.43 (0.04)
3	3	0.42 (0.10)	0.45 (0.05)
4	2	0.41 (0.09)	0.45 (0.07)
5	1	0.34 (0.06)	0.38 (0.04)
6	0	0.38 (0.08)	–

FIG. 7.6. Mean dry matter weights per pot of _C. monilifera_ (□)
and _A. longifolia_ (O) in a replacement series with a
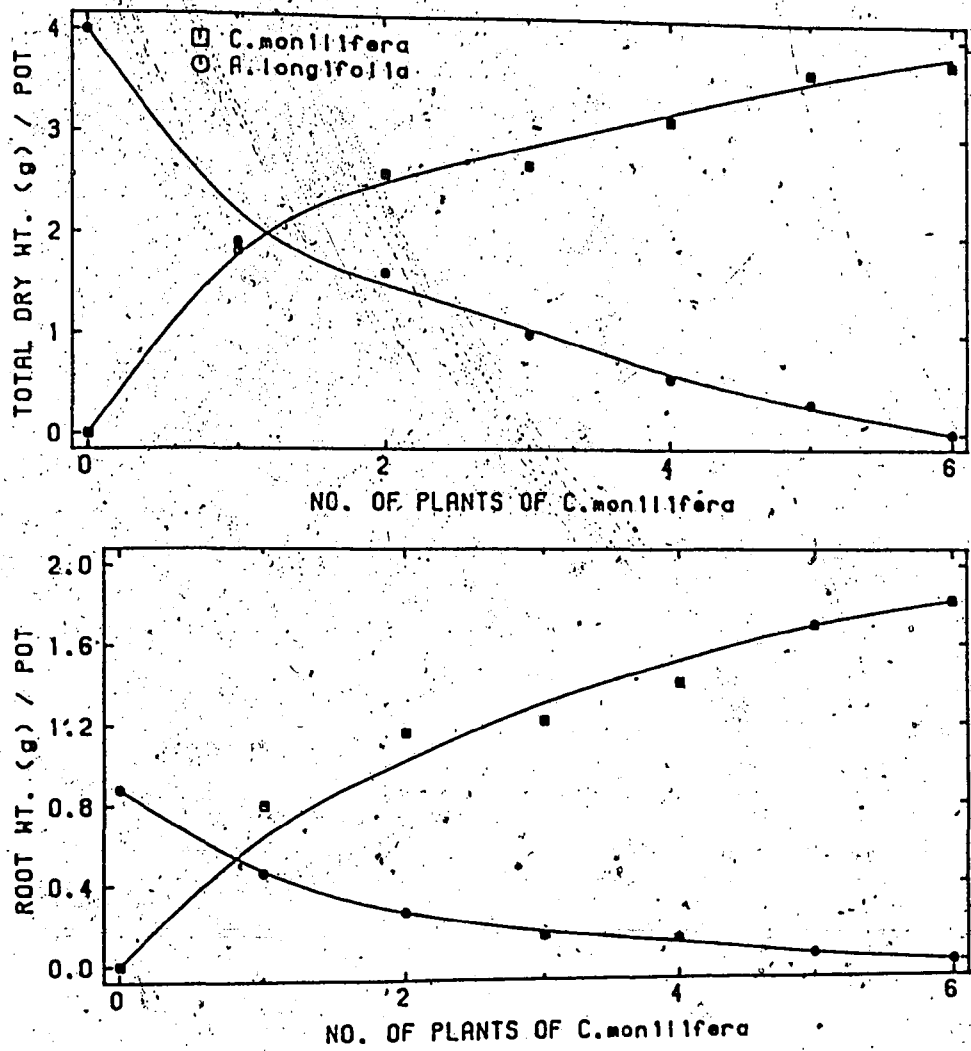constant density of six plants per pot, under water
stress.

FIG. 7.7. Total dry matter weights and root weights per pot of
C. monilifera and A. longifolia in a replacement
series with a constant density of six plants per pot,
under a daily watering regime.

and outcompete A. longifolia. There was a trend for glucose but surprisingly not starch concentration to be reduced with increasing water stress but plants were still comparatively young when measured at the first harvest in the "tube" experiment.

It is clear from the "time" experiment that seedlings of A. longifolia, are better adapted to survive water stress than C. monilifera; the competitive advantage of C. monilifera over A. longifolia is reduced, but not reversed under water stress ("wilt" experiment). The reason for the poorer survival of C. monilifera ("time" experiment) appears to be that it transpires faster which was also shown in the experiments in Chapter 8. These demonstrate a greater transpiration of C. monilifera than A. longifolia at high leaf water potentials but, due to stomatal closure by C. monilifera, this is reversed at low leaf water potentials. Although soil water potential was not measured, it should be more negative in pots containing C. monilifera, at least until stomatal closure. Where water stress was insufficient to cause plant mortality ("wilt" experiment), there would be less available soil water per plant in monocultures than at lower densities. This was apparently responsible for the leaf death and lower than expected weight per pot of C. monilifera in monocultures under water stress.

C. monilifera has higher leaf water potentials in mixtures with A. longifolia than in monocultures (Chapter 8) and so would transpire longer in mixtures. This would leave less available soil water for A. longifolia in mixtures than in monocultures which corresponded to its increased mortality in mixtures ("time" experiment).

7.2 Root and shoot competition

7.2.1 Introduction

Gause (1934) considered that two species scarcely ever occupy similar niches but displace each other so each takes possession of certain resources which give it a competitive advantage. These resources are usually considered to be nutrients and water which are competed for by roots and light competed for by shoots. Others such as space are usually not limiting except in extreme cases eg. densely sown root crops.

Donald (1958) concluded that an aggressive species competed more effectively when both means of competition were available to it (light and nutrients or light and water). The effect of the two modes of

competition on the suppressed species showed a positive interaction. However, one mode of competition may be more important than the other. In a comparison of two closely related species, Emex australis and E. spinosa, Weiss (1977) found that root competition, but not shoot competition, caused a decrease in total weight of seeds of the suppressed species, E. australis.

The purpose of this section was to investigate the relative importance of root and shoot competition between C. monilifera and A. longifolia. I did this by comparing the effects of competition for light, with that for nutrients. Competition for water was eliminated by ensuring all treatments received adequate water since results of the previous section showed that competition for water reduced interactions between the two species.

7.2.2 Methods

Pots and partitions were arranged in a similar manner to that described by Weiss (1977). Root partitioning was achieved by placing four small pots (12.5 x 10.5 cm) inside one large pot (25 x 21 cm) and root competition was achieved by using only large pots containing the same total amount of soil as the four smaller ones. Light competition was eliminated by using two vertical plywood partitions, covered with alfoil and placed at right angles on the soil surface. Additional partitions were used as necessary as the plants grew. Combinations of the above gave either full or no competition. The effect of the small pots and partitions on plant growth was checked by growing monocultures of each species in both the full and no competition arrangements. There were eight plants in large pots and two in each small pot, with three replications of each treatment.

The pots were watered daily to approximately field capacity. Three months after emergence, all plants were harvested. Leaves, stems and roots were separated, leaf area measured and all components oven-dried and weighed.

7.2.3 Results

There were no significant differences in plant weights in the monocultures between the full and no competition arrangements. Compared to no competition, full competition significantly reduced each plant component of A. longifolia and increased each one of C. monilifera (ANOVA, $P \leq 0.05$) (Table 7.6). In the case of total dry matter and leaf and root weights, a 2-way ANOVA showed a significant

Table 7.6 Total dry matter, leaf, stem and root weight and leaf area per plant of C. monilifera (C) and A. longifolia (A) under various modes of competition in the glasshouse

Species	Monocultures		Mixtures		
	No competition	Root + shoot competition	Shoot competition	Root competition	Root + Shoot competition
			Total dry matter (g/plant)		
C	0.91	1.13	1.57	1.76	2.14*
A	0.74	0.92	0.92	0.57	0.43*
			Leaves (g/plant)		
C	0.41	0.43	0.64	0.88	1.00*
A	0.37	0.49	0.44	0.37	0.21*
			Leaves (cm^2/plant)		
C	68	62	83	181*	153*
A	36	50	44	40	22*
			Stems (g/plant)		
C	0.14	0.14	0.22	0.38*	0.34*
A	0.14	0.20	0.19	0.15	0.11*
			Roots (g/plant)		
C	0.40	0.54	0.71	0.43	0.81*
A	0.23	0.23	0.29	0.13*	0.10*

* Significantly different from the monoculture treatments in each row (ANOVA, $P \leq 0.05$)

interaction between root and shoot competition. Root weight of
A. longifolia was also significantly reduced under root competition,
with a trend for the other components measured to be reduced more
under root than shoot competition. When competition was absent, there
was little difference between the two species in stem and leaf
production but root production was greater in C. monilifera.

7.2.4 Discussion

The importance of root competition in deciding the outcome of
interactions between C. monilifera and A. longifolia indicates that
the rate of root development of C. monilifera is a key factor in its
success. However, the interaction of root and shoot competition in
this experiment indicates that light is also important and root
competition by C. monilifera may act initially to suppress
A. longifolia which reinforces later shoot competition. Such a
hypothesis has also been put forward by Harper (1964) who suggested
that the role of water and nutrients "lies often in modifying the
timing and extent of an ultimate struggle for light".

In invaded coastal dunes, competitive effects by C. monilifera on
A. longifolia may be greater than in the pot experiments in this study
because:

(i)   seedlings of A. longifolia are likely to be outnumbered by
      those of C. monilifera

and (ii) they may, in addition, have to compete with adult plants of
      C. monilifera or, in burnt areas, resprouting from adult
      plants of C. monilifera (Chapters 6, 10).

However densities are usually less in the field (than the $350-450 \text{ m}^{-2}$
in the pot experiments), which would decrease competitive effects.

7.3 Field competition

7.3.1 Introduction

In order to determine if competitive effects observed in the
glasshouse were also evident in the field and to eliminate the
disparity in numbers usually seen in Acacia communities invaded by
Chrysanthemoides (Chapter 5), I conducted a replacement series
experiment with C. monilifera and A. longifolia. I did this in both a
burnt and an unburnt area since nutrients and moisture are likely to
vary in their availability between these areas. This may be important
since competitive effects may depend on the resource being competed

for under the prevailing environmental conditions. Dawson (1970) found that the competitive effects of weeds were likely to occur at an earlier stage if moisture rather than light was the primary limiting resource.

7.3.2 Methods

A mid-dune area at Moruya, burnt by a wildfire in September 1980 and an adjacent, similar but unburnt area were selected and a randomised design of plots, each 0.5 x 0.5 m, was laid out. Untreated seeds of C. monilifera ssp. rotundata and seeds of A. longifolia treated with boiling water were used. A total of 100 seeds were sown in early November 1980 at a depth of 2 cm in each plot, consisting of 0, 50, 100 seeds of C. monilifera and the complement of these numbers with respect to 100 of A. longifolia. There were five replications. Plots were watered (8 mm) immediately after sowing and a further 8 mm applied the next day, and 1 and 2 weeks later. Rainfall from November to January averaged 46 mm per month, followed by 210 mm in February 1981 (Fig. 5.4). Counts of emerged seedlings were made at approximately fortnightly intervals until the end of April 1981. Plants were harvested at ground level in early December 1981, dried and weighed.

7.3.3 Results

Emergence of seedlings commenced in early January 1981 and continued until the end of April. There was a comparatively low emergence of both species until after heavy rain in mid-February, when there was a five-fold increase in the number of C. monilifera seedlings in the burnt area compared with the number previously emerged (Fig. 7.8). This final density (60 m^{-2}) was within the range normally found in accessions of C. monilifera. The end result was that, overall, there were 2.5 times as many seedlings of C. monilifera as A. longifolia.

In the unburnt area, emergence and growth of both species remained poor with comparatively high mortality, since it was in an open, exposed site to avoid seed contamination, and so this part of the experiment was discontinued.

Uneven emergence of plants both in time and between plots precluded a detailed analysis of the dry weight data. However, density-dependent trends in dry weight per plant are apparent in Fig. 7.9. Only data from plots with comparatively even emergence with
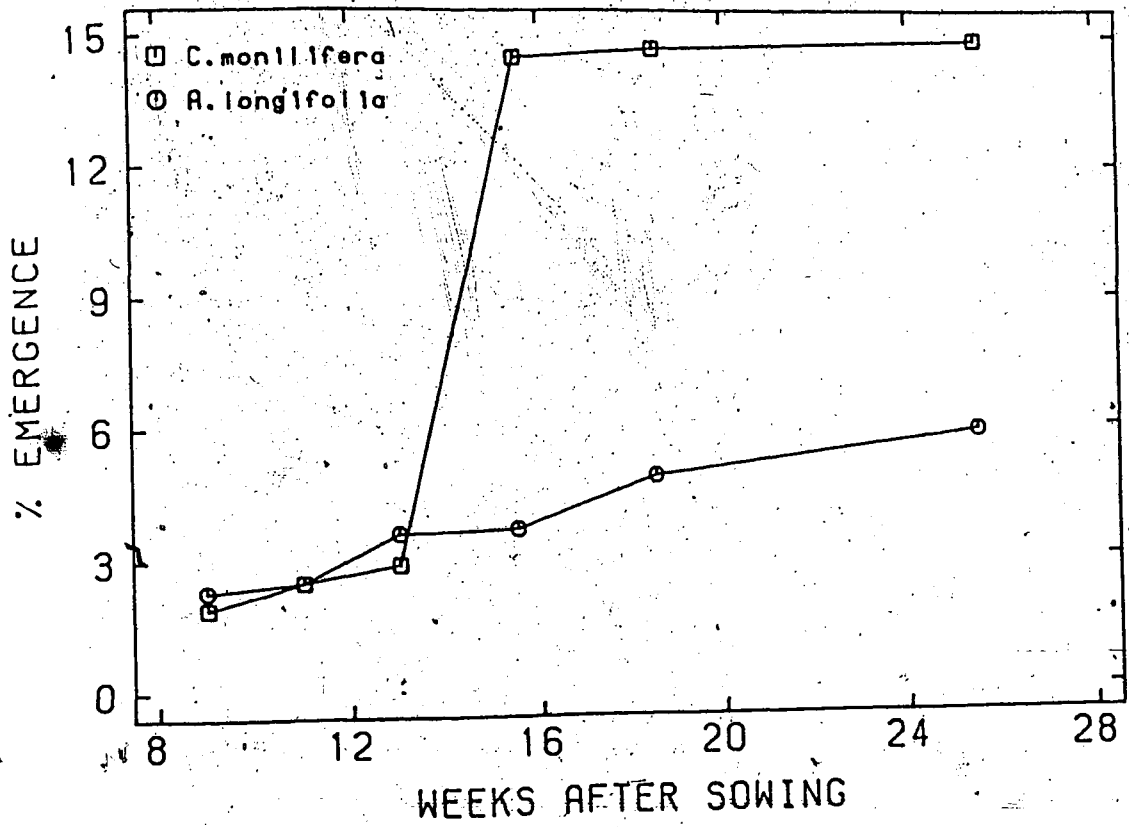
FIG. 7.8. Mean cumulative percentage emergence of C. monilifera
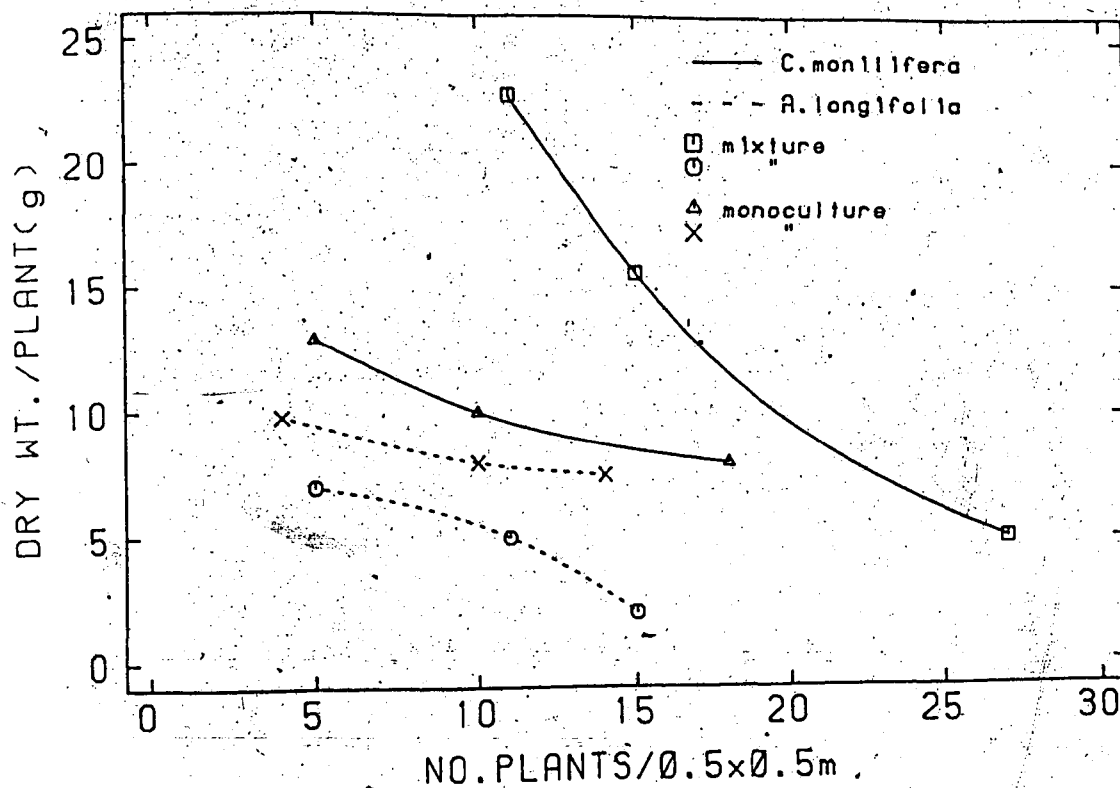and A. longifolia in the field experiment.

FIG. 7.9. Total dry matter weights per plant of C. monilifera
and A. longifolia in monocultures and mixtures at a
range of densities in the field experiment.

time are shown.

The enhanced growth of C. monilifera and the depression of A. longifolia in mixtures is clear. Some mortality of A. longifolia occurred in mixtures at low densities where growth of C. monilifera was vigorous such that it had flowered and set viable seed by the time of harvest. All plants of A. longifolia were still in the vegetative stage at the end of the experiment.

7.3.4 Discussion

The marked competitive advantage of C. monilifera over A. longifolia in the burnt area, where resources are comparatively good, parallels that in well-watered conditions in the glasshouse (section 7.1). The effect of intraspecific competition on C. monilifera is more pronounced than interspecific. That is, a given plant, of C. monilifera grows better if its neighbour is A. longifolia rather than C. monilifera.

The growth of C. monilifera is density dependent. Thus, although burning reduces the number of subsequent seedlings of C. monilifera (Chapters 4, 10), total biomass per unit area is unlikely to be correspondingly reduced. The precocious growth of C. monilifera in burnt areas, especially at low seedling densities, poses a control problem in that the seed population is capable of being replenished within a period of 12 months from seedling emergence.

7.4 Seed production of A. longifolia

7.4.1 Introduction

The previous experiments in this chapter have demonstrated a competitive effect between Chrysanthemoides and Acacia at the seedling stage and it is possible that once A. longifolia reaches maturity, it may not be affected by competition from C. monilifera or at least not to the same extent. Alternatively, the opposite may occur — C. monilifera may act in such a way as to dilute the effects of predators on A. longifolia by interfering with their orientation and utilisation. Thus Root (1974) considered that ecosystems in which plant species are intermingled possess an "associational resistance" to certain types of herbivores. C. monilifera may also act as a repellant for predators of A. longifolia by virtue of the cyanogenic glycosides, linamarin and lotaustralin, which are present in its leaves (Conn 1981). I therefore investigated the effect of natural

populations of mature plants of C. monilifera on those of nearby A. longifolia both in relation to seed production and extent of predation.

7.4.2 Methods

Forty mature plants of A. longifolia were selected in early December 1981, 20 growing at least 10 m from the nearest plant of C. monilifera ("-" treatment) and 20 in the same vicinity but intermingled with mature plants of C. monilifera ("+" treatment). One stem, with a maximum diameter of 2.0 ± 0.1 cm, was selected on each plant of A. longifolia. All pods (which were unopened) were harvested from this stem, seeds removed and counted in each pod and total seed weight per stem and weight per 100 seeds obtained. The numbers of parasitised and empty seeds were estimated by taking a sub-sample of 200 seeds from each lot and cutting them open. Results were analysed by t-tests on each of the parameters measured.

7.4.3 Results

There were no significant differences in any of the various seed production parameters measured in A. longifolia between the + and – treatments (t-test, $P > 0.05$) (Table 7.7). However, there was a trend in each case for larger seed weights and numbers and lower percentages of parasitised and empty seeds in the – treatment compared with the + treatment.

7.4.4 Discussion

It is difficult in this experiment to separate effects of direct competition with C. monilifera and any dilution of predator influence by C. monilifera on seed production of A. longifolia. In any case, there was no evidence of predator protection by C. monilifera perhaps because the most obvious predators affecting seed yield of A. longifolia are specialists (Trichalogaster longifolia and Melanterius sp.) which attack only developing pods and seeds. In fact, there was a trend in the opposite direction, ie more predation in the mixtures. This may have been due to some protection from wind, sand and salt blast being afforded by the canopy of C. monilifera to insects while locating their host and completing their life cycle on A. longifolia.

Table 7.7 Seed production of A. longifolia when growing away from or
when mixed with C. monilifera. Standard errors are in
parentheses

Attribute	- C. monilifera	+ C. monilifera
No. of pods per stem	149.4 (23.0)	144.3 (30.5)
No. of seeds per stem	641.5 (109.6)	573.3 (124.8)
No. of seeds per pod	4.23 (0.22)	4.00 (0.18)
Seed wt. per stem (g)	18.23 (4.1)	15.56 (3.7)
Wt. per 100 seeds (g)	2.69 (0.20)	2.65 (0.17)
Parasitised seeds (%)	11.3 (2.6)	16.8 (4.0)
Empty seeds (%)	26.4 (4.4)	38.6 (4.8)

Although there was no significant yield depression in
A. longifolia when growing with C. monilifera, there was a trend in
this direction in all of the five seed parameters measured. This
implies that the number of plants measured was insufficient. However,
it can be calculated from the magnitude of the standard errors that
over 20 times as many plants would require to be sampled for
significance and practical considerations precluded this number. In
any case, the differences were not large between the + and
- treatments and I conclude that competition is less pronounced at the
reproductive than at the seedling stage.

7.5 Allelopathy

7.5.1 Introduction

It has been argued (Swain 1977) that it is unlikely that the
diverse nature of secondary chemical compounds in higher plants lacks
ecological significance. Muller (1966), in his review, discussed the
role of allelopathy in vegetational composition and later reports
confirmed the significance of such an effect in some natural plant
communities (Muller 1969; Rovira 1969; Rice 1974).

It might be expected that allelopathy could be a factor in the
success of an invasive species such as C. monilifera, which led to the
present experiments. The majority of allelopathic studies have used
extracts from living or dead plant material to test germination of
seeds. This often results in seeds receiving concentrations of
phytotoxins higher than those normally found in the field. I tested
leaf, litter and seed leachates from C. monilifera on germination of
seeds of A. longifolia and also carried out a field experiment in
which, however, I did not attempt to resolve the difficulty of
separating allelopathic, competitive and environmental effects
associated with C. monilifera.

7.5.2 Methods

Laboratory experiments

Water-soluble leachates were prepared in a manner similar to that
described by Stout & Tolman (1941). Lots of either 25, 50, 100, 200,
400 seeds or leaves (50 g) of C. monilifera were collected from the
field, surface sterilised in a 0.1% solution of silver nitrate of
three times their volume, washed with water and each left in 50 ml
water for 24 h. Then 5 ml of this leachate was added to each of four

petri dishes containing filter paper and ·25 cut seeds of A. longifolia. Germination was recorded after 4, 8 and 12 days.

Germination of seeds of A. longifolia was also tested firstly with lots of 20 seeds mixed with 20 seeds of C. monilifera in petri dishes; secondly, with seeds placed on moist filter paper with litter of C. monilifera beneath it in petri dishes; and thirdly, with seeds sown in sand with litter of C. monilifera on the surface in pots.

Field experiment

Ten mature plants of C. monilifera and A. longifolia were selected at Moruya and 100 seeds of each species sown (after a boiling water treatment of A. longifolia) near the centre of each plant, between the centre and edge of the canopy, at the edge of the canopy and 1 m and 2 m outside the edge. The sand in each area was first sieved to remove any seeds already present. Germination was recorded at monthly intervals for 4 months.

In all experiments, percentages were arcsine transformed before ANOVA analysis (Sokal & Rohlf 1969, p.386). Untransformed numbers are given in the results.

7.5.3 Results

Laboratory experiments

There were no significant differences (ANOVA, $P > 0.05$) between germination of seeds in the seed and leaf leachates and controls (Table 7.8).

Similarly, the presence of seeds or litter of C. monilifera in petri dishes or pots had no significant effect on germination of seeds of A. longifolia. However, seedling vigour was visibly less in pots with litter than without.

Field experiment

Emergence of seedlings of both species was less under mature plants than at the edge of the canopy or in the open (Table 7.9).

Table 7.8 Mean percentage germination of seeds of _A. longifolia_ at
three times after addition of seed or leaf extracts of
C. monilifera

Source of leachate	Germination of _A. longifolia_ (%)		
	4 days	8 days	12 days
25 seeds	32	68	72
50 seeds	27	62	82
100 seeds	30	72	84
200 seeds	28	66	78
400 seeds	21	58	74
Leaves	25	60	82
Control	30	72	88

Table 7.9 Mean percentage emergence of seedlings of <u>C</u>. <u>monilifera</u> (C) and <u>A</u>. <u>longifolia</u> (A) after 4 months from seeds sown at varying distances in relation to the centre of mature plants of <u>C</u>. <u>monilifera</u> and <u>A</u>. <u>longifolia</u>. Standard errors are shown in parentheses

Position in relation to mature plants	Mature C. monilifera		Mature A. longifolia	
	C (%)	A (%)	C (%)	A (%)
Near centre	3 (0.9)	1 (0.4)	5 (2.6)	4 (1.2)
Between centre and edge	8 (2.3)	6 (1.9)	13 (5.8)	7 (3.5)
Edge	15 (3.5)	17 (3.9)	18 (7.6)	12 (3.8)
1 m outside	12 (3.1)	13 (3.7)	20 (9.3)	15 (4.0)
2 m outside	14 (4.2)	12 (4.7)	18 (8.4)	14 (6.5)

7.5.4 Discussion

There was no significant evidence from the laboratory experiments that the germination of seeds of A. longifolia was adversely affected by litter or leachates from seeds or leaves of C. monilifera. In the field experiment, seedling numbers from sown seeds at the canopy edge were generally as high as outside the canopy. The lower numbers near the centre of mature plants may have been due to emergence and death of some seedlings before counts were made. Mortality may also have been due to the heavy litter fall (Chapter 3) and low light intensity under mature plants.

In natural populations, most seedlings of C. monilifera are found under the canopy of parent plants (Fig. 2.2) because of the concentration there of the soil seed pool (Chapter 3). The few seedlings of A. longifolia that were present in natural populations were also found under or at the edge of mature plants, including individuals of C. monilifera (Fig. 2.2).

I conclude that the lack of a laboratory effect by leachates of C. monilifera on germination of A. longifolia makes it unlikely that allelopathy is implicated in such interactions in the field and there was no evidence of this from the field experiment. However, while competitive effects from C. monilifera would reinforce any allelopathic influence, the presence of C. monilifera could have a protective effect on seedlings and so counteract any allelopathy.

7.6 Summary

The results from this and previous chapters indicate that the success of C. monilifera in competition with A. longifolia may be attributed in part to the former species having:

1. Faster germination than A. longifolia under adverse soil moisture conditions (Chapter 4);

2. The ability to develop a large leaf assimilation surface in the early seedling stage (Chapter 6); and

3. A large mass of fibrous roots close to the soil surface, but a deeply penetrating main root (section 7.1).

The effect of water relations on growth and outcome of competition between the two species is evident (Table 7.10) and this aspect was investigated further in physiological studies in the succeeding chapters 8 and 9. However, it should be pointed out that other factors such as competition for nutrients and light can be important, especially since both species exist under low moisture conditions in their native habitats and are presumably adapted to such conditions.

Table 7.10   Summary of results of competition experiments between
C. monilifera (C) and A. longifolia (A)

Parameter	Experimental result
Total dry weight of seedlings	C outcompetes A when well watered but the effect is minimised under water stress. Root competition is more important than shoot competition but there is interaction between the two.
Roots of seedlings	In monocultures, roots are heavier and more extensive in C. In mixtures, root weight of A is reduced.
Glucose and starch in seedlings	A has more carbohydrate per unit dry weight of shoots than C in both monocultures and mixtures. There is little difference between species in carbohydrates in roots which have a smaller concentration than in shoots.
Mortality of seedlings	In monocultures, there is less mortality of A than C when under prolonged water stress, with little difference in mixtures.
Seed production	There is a trend towards lower seed numbers and weights and higher seed predation of A in mixture with C.
Allelopathy	There is no evidence in laboratory experiments of an allelopathic effect of C on germination of seeds of A.

Chapter 8

Water relations of <u>Chrysanthemoides</u> and <u>Acacia</u> under controlled conditions

"The plant invaders advance remorselessly across the Cape countryside, choking rivers, dams and irrigation channels; starving our indigenous flora of water, light and air."
(Stirton 1978)

"Water stress affects virtually every aspect of the physiological and metabolic activities of the plant. All available evidence indicates that drought tolerance is related to the environment to which the plants have adapted and any correlation with photosynthetic or taxonomic type is likely to be indirect."
(Osmond, Bjorkman & Anderson 1980)

Introduction

The growth of coastal sand dune communities takes place in an edaphic environment which is characteristically low in water and nutrients. Plants growing in xeric environments have evolved a number of drought resistance mechanisms (Parker 1969, Levitt 1972). Levitt divided drought avoiders into "water savers" which avoid drought by water conservation, and "water spenders" which absorb water rapidly enough to compensate for their rapid water loss. Water spenders usually compete strongly for soil water when this is low. Water savers are less dependent on soil water reserves since they have efficient control of water loss and the ability to tolerate very low xylem pressure potentials (Shea, Bartle & Richmond 1979). These authors point out that both water savers and spenders can be found within the same plant community. Different patterns of water use may contribute to a niche differentiation of species growing in the same habitat.

It might be expected that plants invading xeric environments have characteristics akin to water spenders which enable them not only to survive but even to become a dominant member of the community by competing successfully for resources such as water. However, this does not always apply. In a study of an exotic species (Pinus radiata) invading a native Eucalypt forest, Foster (1979) attributed part of the success of the invader being a water saver, having lower transpiration and intercellular conductance than E. rossii. Stomatal closure occurred at a higher leaf water potential in P. radiata which also showed higher dawn leaf water potentials than E. rossii. Since leaf water potential gives some indication of plant water status (Lange 1975), it appears that the early closure of the stomates of P. radiata is effective in controlling water loss.

The superiority of C. monilifera when competing with A. longifolia is more marked under well-watered than water-stress conditions. In order to investigate the reasons for the observed outcome of such competition, I determined first their physiological characteristics at one time when competing with each other in controlled environments. Second, I investigated their characteristics at several times during development of and recovery from stress. Finally, I measured in each species the relationship of water potential to relative water content and obtained estimates of

osmotic potential.

8.1 Competition

8.1.1 Introduction

Recently, Pearcy, Tumosa & Williams (1981) compared growth and photosynthesis of competing C_3 and C_4 plants, represented by Chenopodium album (fat-hen) and Amaranthus retroflexus (amaranth) respectively. They found that C. album had a higher photosynthetic and relative growth rate in monocultures and outcompeted A. retroflexus in mixtures at temperatures under 25°C. On the other hand, the reverse was true at temperatures over 25°C (A. retroflexus was superior). Limited water supply had no effect on the competitive interactions.

However, both C. monilifera and A. longifolia are C_3 species and although photosynthesis is undoubtedly important in most cases, Werner (1981) found other factors decided the outcome of competition in Solidago spp. In co-occurring S. canadensis and S. juncea (goldenrods), assimilation rates per unit leaf area and water use efficiencies (the ratio of transpiration to assimilation) were similar. However, S. canadensis outcompeted S. juncea, probably because of differences in leaf area and phenology. In order to determine if a similar situation occurred in the case of Chrysanthemoides and Acacia, I carried out gas exchange measurements on seedlings of each species in the "tube" experiment in which both water stress and no stress were present (Chapter 7).

Since various physiological parameters are related in the equation:

$$C_i = C_a - (1.6\ A/g)$$

where C_i = partial pressure of intercellular CO_2;

C_a = partial pressure of CO_2 in the air;

A = assimilation rate; and

g = stomatal conductance rate,

I measured each of these, as well as transpiration rate and, in one treatment, determined the relationship between light and assimilation rate.

8.1.2 Methods

Gas exchange measurements were carried out on both monocultures and mixtures of C. monilifera and A. longifolia in the "tube" competition experiment (Chapter 7). There were either 0 (sub-irrigation), 1, 6 or 12 days between water applications. Measurements were made the day before watering on 2-month old plants in each of the three replicates on the youngest, fully expanded leaf or phyllode. Details of the gas exchange apparatus and method of use are given in Appendix 2. Measurements were made at 40% of full sunlight since most seedlings are shaded by mature plants in the field. However, one treatment was selected (monocultures watered at 6 day intervals) to determine the effect of a range of light intensities up to full sunlight on assimilation rate.

8.1.3 Results

Assimilation, transpiration and conductance were reduced in both species when water was withheld for 6 or 12 days (Table 8.1). Assimilation rate was over 50% greater in monocultures of A. longifolia than C. monilifera under all watering regimes. However, whereas the assimilation of C. monilifera was little changed in mixtures, that of A. longifolia fell to be about the same as that of C. monilifera. There was a trend for rates of conductance and transpiration of A. longifolia in both monocultures and mixtures to be less than those of C. monilifera when well-watered, but the reverse generally occurred in the water stress treatments. C_i was generally lower in both species under water stress and was lower in A. longifolia than C. monilifera in all treatments.

Low transpiration to assimilation ratios indicate high water use efficiency. In the well-watered treatments, the ratios were significantly lower in monocultures of A. longifolia than C. monilifera (ANOVA, $P \leq 0.05$) (Table 8.2). There were no significant differences between the species in the water stress treatments. However, lower transpiration to assimilation ratios in A. longifolia were also apparent in linear regressions of assimilation against transpiration over all watering regimes (Fig. 8.1). The regressions shown do not apply to very low values of assimilation and transpiration and in fact should intercept the origin or the x-axis.

Table 8.1 Rates of assimilation, transpiration, conductance, and C_i values in monocultures and mixtures of C.monilifera and A.longifolia grown under four watering regimes (standard errors are given in parentheses)

Time between watering (days)	C.monilifera		A.longifolia	
	Monocultures	Mixtures	Monocultures	Mixtures
Assimilation (μ mol CO_2 m^{-2} s^{-1})				
0	9.6 (0.9)	10.7 (1.5)	17.6 (2.2)	11.0 (1.9)
1	10.0 (0.4)	10.6 (1.4)	15.8 (2.0)	11.6 (2.2)
6	4.9 (0.7)	4.9 (0.8)	9.4 (3.4)	4.0 (1.7)
12	4.3 (1.3)	4.1 (0.9)	13.6 (4.0)	4.0 (1.9)
Transpiration (m mol H_2O m^{-2} s^{-1})				
0	5.4 (0.6)	5.1 (0.5)	4.5 (0.4)	4.6 (0.5)
1	4.8 (0.6)	4.4 (0.7)	4.5 (0.9)	3.1 (0.5)
6	0.7 (0.4)	0.7 (0.3)	2.0 (0.8)	0.9 (0.3)
12	1.1 (0.4)	0.6 (0.2)	2.7 (1.9)	0.8 (0.2)
Conductance (mol H_2O m^{-2} s^{-1})				
0	0.31(0.04)	0.29(0.06)	0.24(0.02)	0.20(0.05)
1	0.26(0.04)	0.24(0.07)	0.23(0.05)	0.15(0.03)
6	0.12(0.07)	0.08(0.02)	0.11(0.05)	0.06(0.02)
12	0.05(0.02)	0.04(0.01)	0.15(0.11)	0.04(0.02)
C_i (m bar)				
0	272 (11)	258 (23)	214 (11)	238 (20)
1	271 (8)	250 (26)	216 (12)	201 (22)
6	210 (33)	220 (19)	200 (5)	212 (17)
12	208 (33)	175 (27)	169 (45)	155 (18)

Table 8.2 Ratios of transpiration to assimilation in monocultures of
C. monilifera and A. longifolia under four watering regimes

Time between watering (days)	C.monilifera		A.longifolia	
0	578	Aa	266	Ab
1	482	Aa	275	Ab
6	143	Ba	207	ABa
12	236	Ba	173	Ba

Values in columns followed by the same upper case letter and in rows
by the same lower case letter are not significantly different
(Duncan's multiple range test, P=0.05).

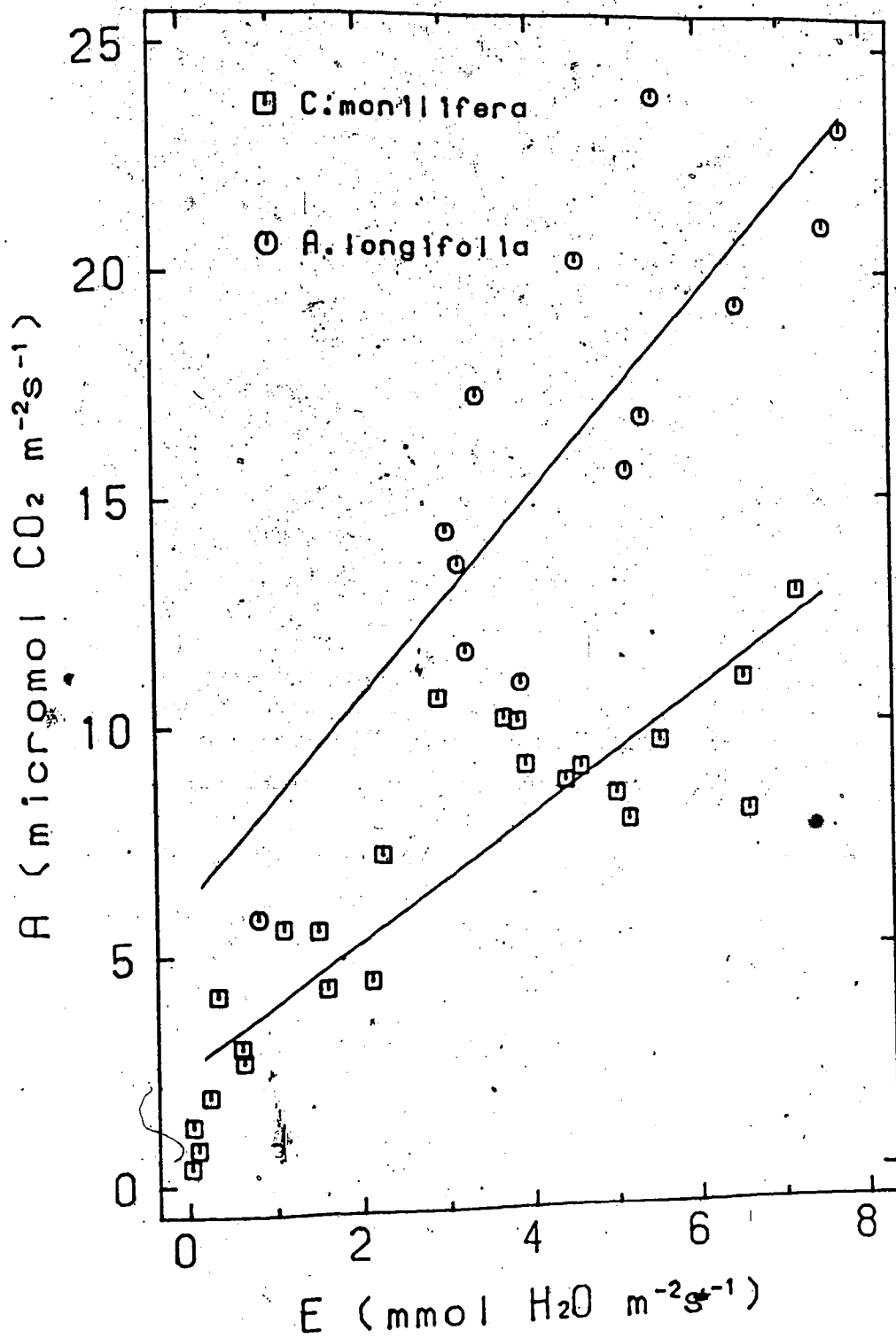FIG. 8.1. Relationship between assimilation and transpiration in
C. monilifera and A. longifolia over a range of watering
regimes (0, 1, 6, 12 days between watering) in the
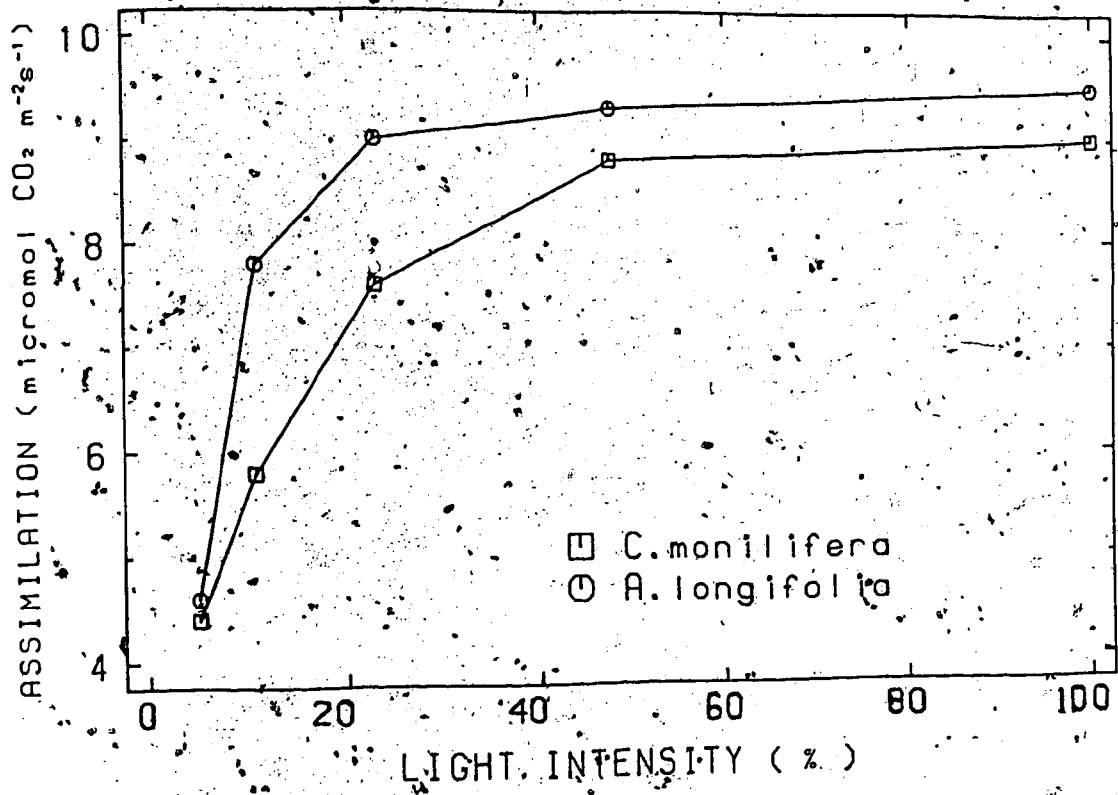glasshouse.

FIG. 8.2. Effect of light intensity (expressed as percentages of full sunlight) on rate of assimilation of seedlings of C. monilifera and A. longifolia.

The assimilation rate of $\underline{C}$. monilifera fell more sharply than that of $\underline{A}$. longifolia at low light intensities (Fig. 8.2).

8.1.4 Discussion

Rates of transpiration and stomatal conductance were greater in $\underline{C}$. monilifera than $\underline{A}$. longifolia when well watered, with the latter having a greater water use efficiency. $\underline{C}$. monilifera transpired less per unit leaf area under water stress than $\underline{A}$. longifolia but total leaf area was approximately three times that of $\underline{A}$. longifolia, so that transpiration per plant was still higher in $\underline{C}$. monilifera. Thus it appears that $\underline{C}$. monilifera and $\underline{A}$. longifolia may be differentiated as a "water spender" and a "water saver" respectively.

Values of C_i were higher in $\underline{C}$. monilifera as would be expected if A were small and g large because of the relationship shown previously (C_a was constant each time):

$$C_i = C_a - (1.6 \, A/g)$$

The higher assimilation per unit leaf area of $\underline{A}$. longifolia in monocultures is consistent with the higher carbohydrate concentrations found in its leaves compared to $\underline{C}$. monilifera (Chapter 7). On the other hand, assimilate produced by $\underline{C}$. monilifera is spread more thinly over a greater leaf area. Leaf growth in $\underline{A}$. longifolia thus appears to be associated with "quality" whereas that in $\underline{C}$. monilifera is associated with "quantity".

It might be expected that leaf longevity would be greater in $\underline{A}$. longifolia and although not reported in this thesis, there was some indication of this from litter-fall in seed traps used in the experiments in Chapter 3.

On a per plant basis, the larger leaf area of $\underline{C}$. monilifera is far greater than that of $\underline{A}$. longifolia (Chapter 6). This would compensate in terms of overall plant assimilation for the lower assimilation rate per unit leaf area of $\underline{C}$. monilifera compared to $\underline{A}$. longifolia. A similar situation occurred in a comparison of the C_3 species, Oplismenus compositus with the C_4 species, Axonopus compressus and Setaria plicata (Hofstra & Stienstra 1977). The disadvantage of a lower assimilation rate per unit leaf area of the C_3 species was overcome by the formation of a larger leaf area so that there were no large differences between the C_3 and C_4 species in relative growth rates.

The greater leaf area of C. monilifera would be of benefit in leading to a "shading strategy" since this would give it an advantage in competition for light. This may be necessary since assimilation rate in C. monilifera drops more sharply than that of A. longifolia at low light intensities (Fig. 8.2) and so more light would be needed by the former to maintain its competitive advantage. It may also help to explain the propensity of mature plants of C. monilifera to "climb" over other species.

The greater water use efficiency of A. longifolia was apparent only in the well-watered treatments (Table 8.2) which may have been due to earlier stomatal closure by C. monilifera as stress developed in the other treatments. This and recovery from water stress which may be important in survival was investigated in the next section.

8.2 Development of and recovery from water stress

8.2.1 Introduction

Since some plants can tolerate water stress (Begg & Turner 1976), it might be expected that there would be differences in the rate and extent of recovery of photosynthesis and that it may be influenced by the amount of stress experienced. In Panicum maximum (guinea grass), the rate of recovery of photosynthesis was slower the greater the stress experienced, but the extent of the recovery was not affected (Ludlow, Ng & Ford 1980).

Recovery of water potential varies between species. In P. maximum, more stressed leaves (below -4 MPa (-40 bars)) had a slower rate of recovery of water potential than less stressed leaves (Ludlow, Ng & Ford 1980). However, Boyer (1971) found that leaf water potential of Helianthus annuus (sunflower) showed no sign of recovery once potentials had declined to -2 MPa (-20 bars) or below during desiccation.

I investigated the gas exchange characteristics and leaf water potentials of C. monilifera and A. longifolia during the course of several drying cycles since drying, at least near the surface, would be expected to occur rapidly on sand dunes.

8.2.2 Methods

Pre-germinated seeds of C. monilifera and A. longifolia were sown in sand in 25 cm diameter pots either in monocultures of 12 plants per pot or in mixtures of six plants of each species per pot. After establishment, the pots were allowed to dry out until the first sign of wilting when all pots were watered to field capacity. There were six such drying cycles, with up to 18 days between waterings. Measurements of gas exchange using the same leaf and the first fully expanded leaf were made during each cycle.

Leaf water potentials were measured at dawn at 1 to 3 day intervals during the second, third and sixth cycles with a "pressure bomb", similar to that described by Ritchie & Hinckley (1975). The system entailed applying a positive pressure to the leaf and finding the force needed to extrude water from the cut petiole (Scholander, Hammel, Bradstreet & Hemmingsen 1965).

Pots were weighed at 1 to 3 day intervals during the first and second drying cycles.

8.2.3 Results

In monocultures, A. longifolia again had a higher rate of assimilation than C. monilifera (Fig. 8.3), but the relative positions were reversed in mixtures (Fig. 8.4). In both monocultures and mixtures, C. monilifera had a higher transpiration rate than A. longifolia except near the end of the drying cycle when stomatal closure was more marked in C. monilifera (Figs. 8.5, 8.6). This occurred at c. -0.8 MPa (-8 bars) in C. monilifera when there was a sharp drop in transpiration; transpiration declined more slowly in A. longifolia up to c. -1.6 MPa (-16 bars) (Fig. 8.7). This was reflected in the highest weight loss in pots containing monocultures of C. monilifera, with the rate of loss decreasing markedly towards the end of the drying cycle (Fig. 8.8). Weight loss in pots containing mixtures was virtually the same as in those with C. monilifera monocultures. This implies that the smaller number of plants of this species in a mixture transpired more per plant than the amount per plant in a monoculture. In fact, size per plant of C. monilifera was greater in mixtures than monocultures.

Leaf water potential as well as transpiration decreased towards the end of the drying cycle; leaf water potential dropped further in monocultures of C. monilifera than A. longifolia (Fig. 8.9).
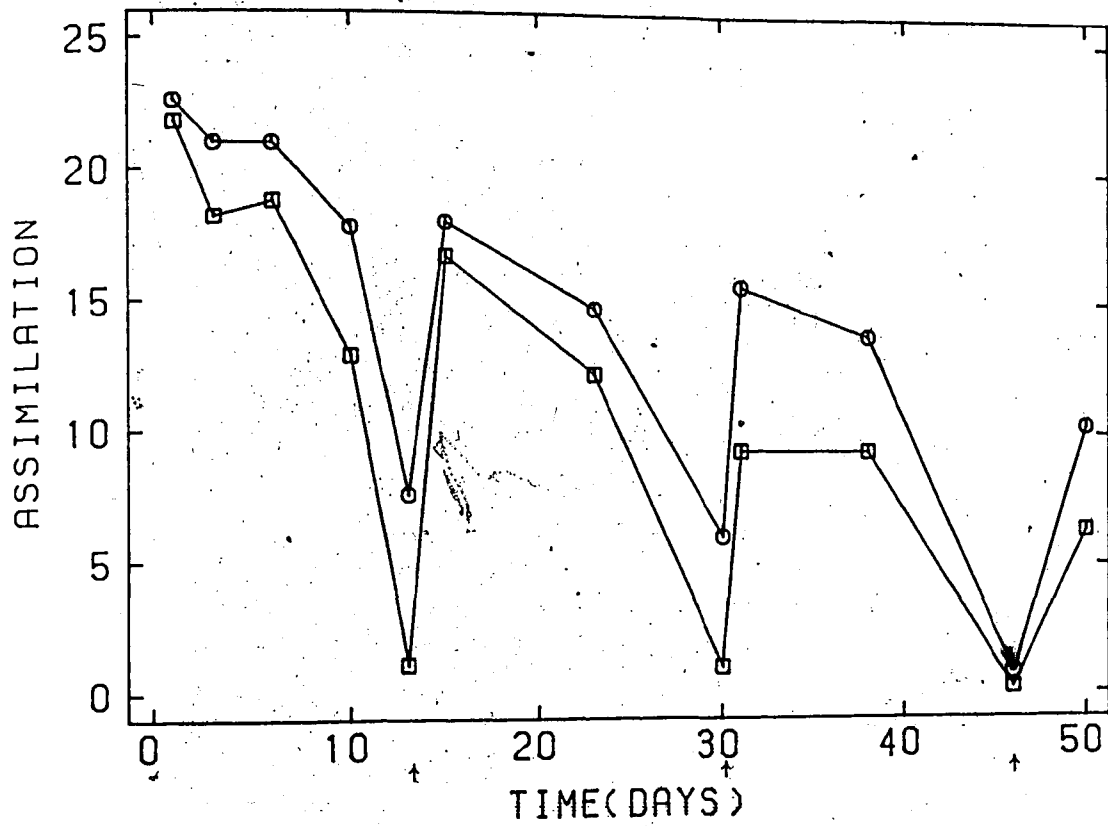
FIG. 8.3. Rates of assimilation (μmol CO_2 m^{-2} s^{-1}) in monocultures of <u>C. monilifera</u> ($\square$) and <u>A. longifolia</u> (O) over four drying cycles. Arrows indicate watering.

FIG. 8.4. Rates of assimilation (μmol CO_2 m^{-2} s^{-1}) in a 1:1 mixture containing C. monilifera ($\square$) and A. longifolia (O) over four drying cycles. Arrows indicate watering.
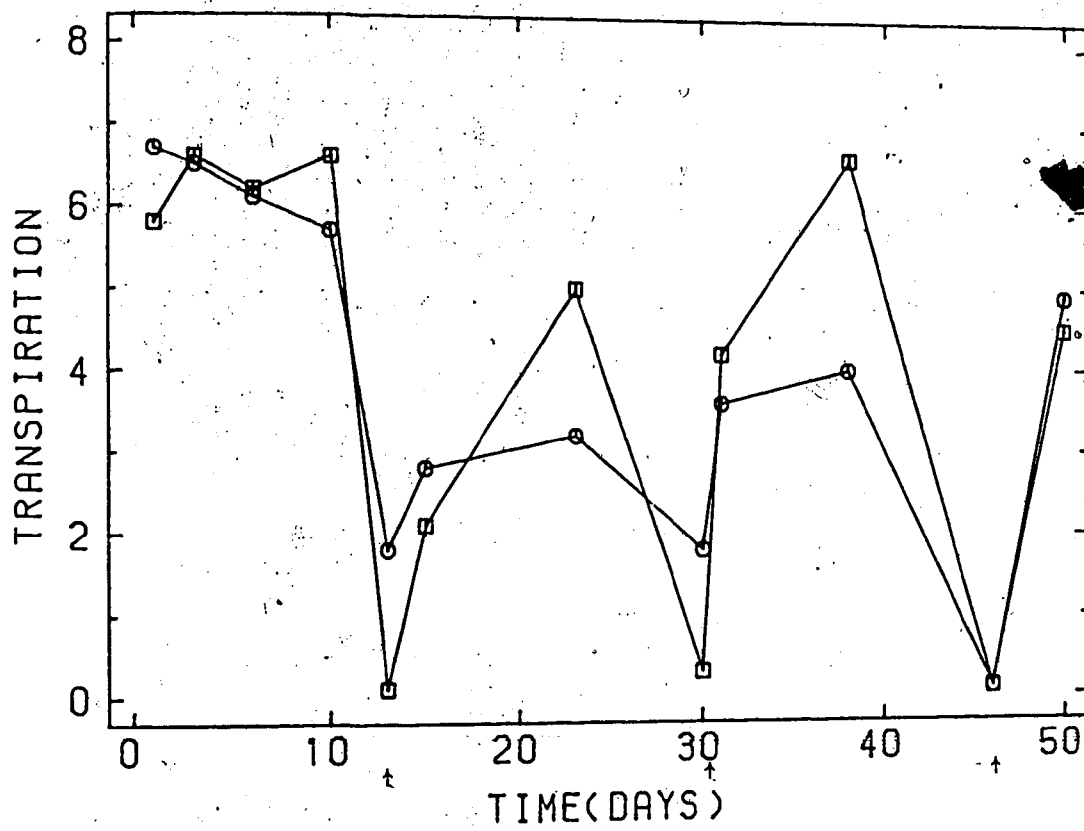
FIG. 8.5. Rates of transpiration $(m\,mol\ H_2O\ m^{-2}\ s^{-1})$ in monocultures
of C. monilifera ($\square$) and A. longifolia (O) over four
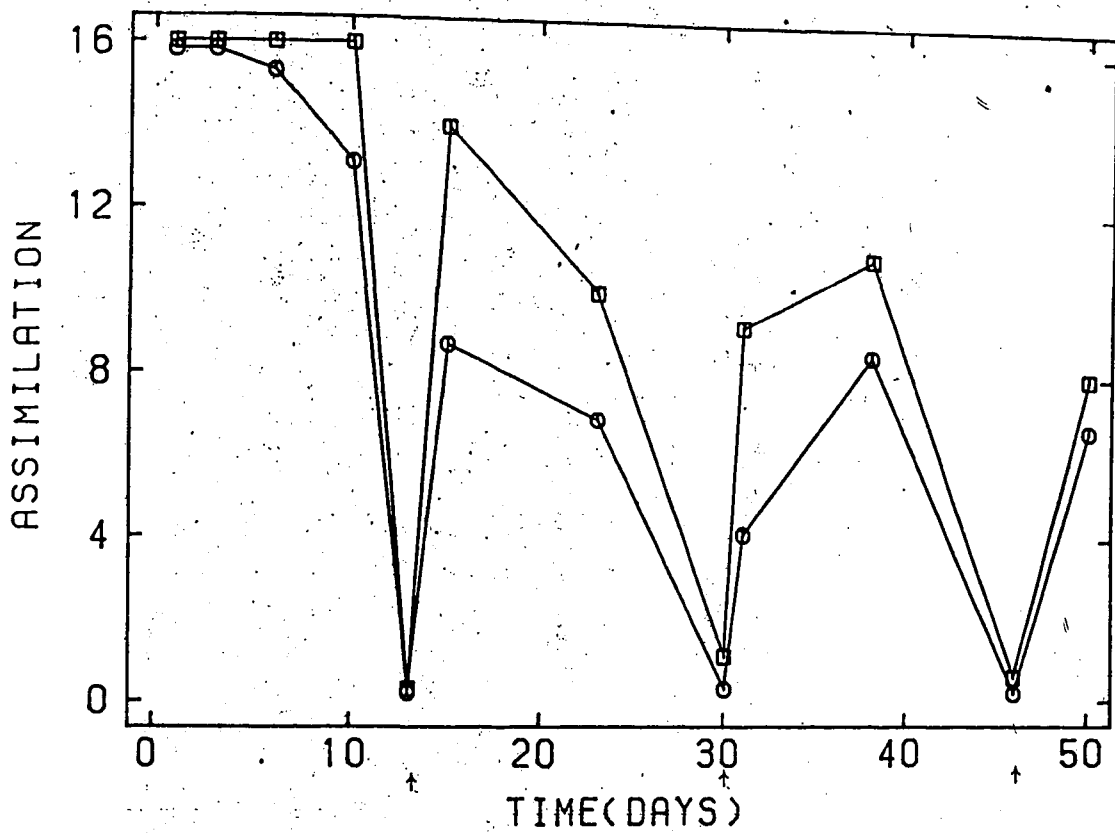drying cycles.   Arrows indicate watering.
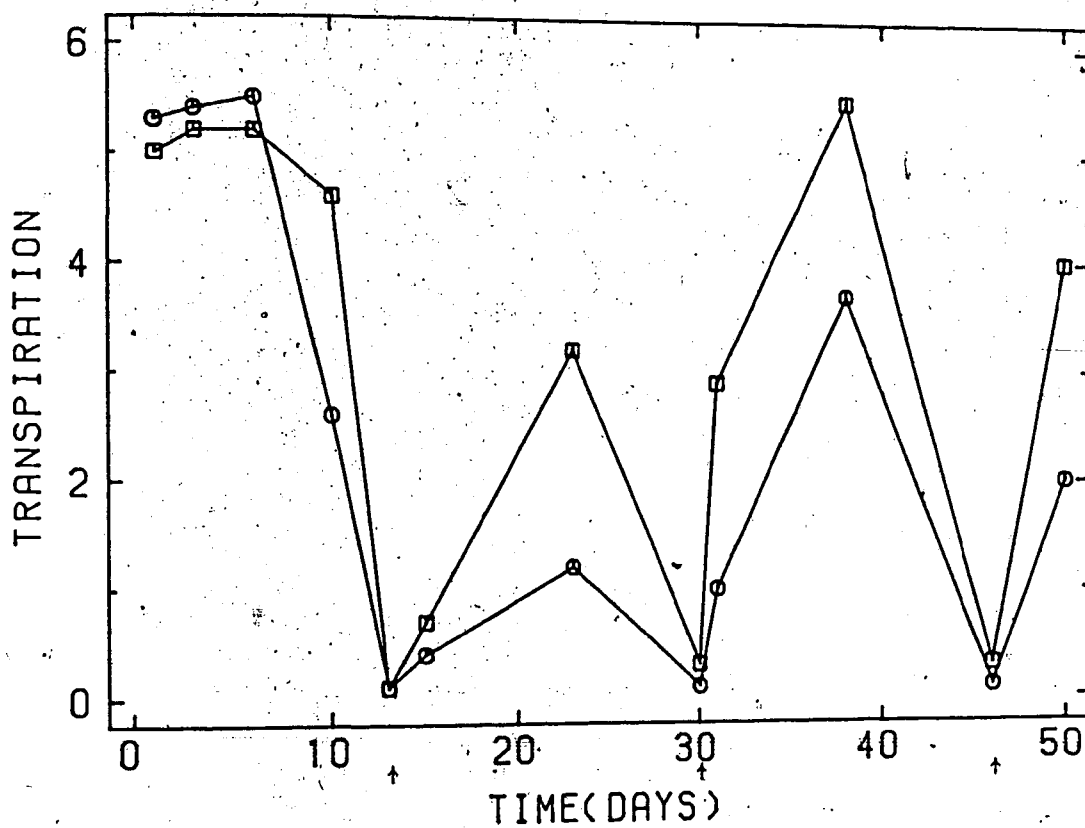
FIG. 8.6. Rates of transpiration (m mol H_2O m^{-2} s^{-1}) in a 1:1 mixture containing _C. monilifera_ (□) and _A. longifolia_ (O) over four drying cycles. Arrows indicate watering.
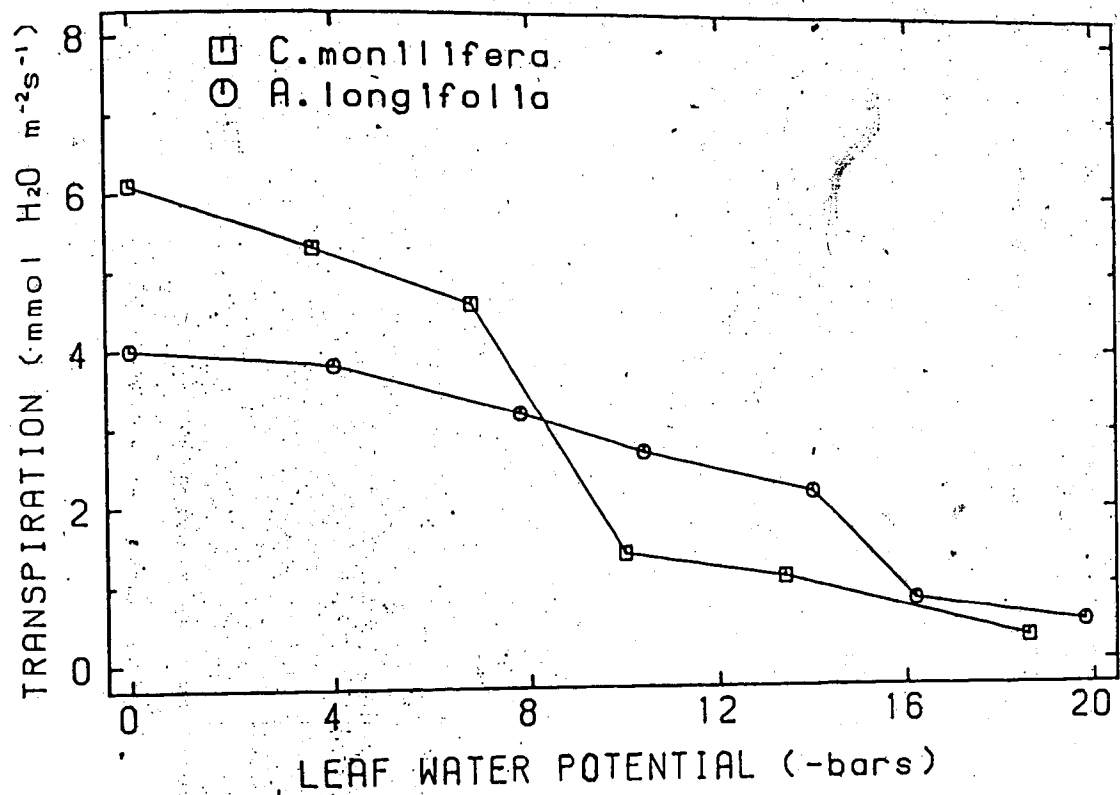
FIG. 8.7. Effect of leaf water potential on rate of transpiration of _C. monilifera_ and _A. longifolia_ (1 MPa = 10 bars).
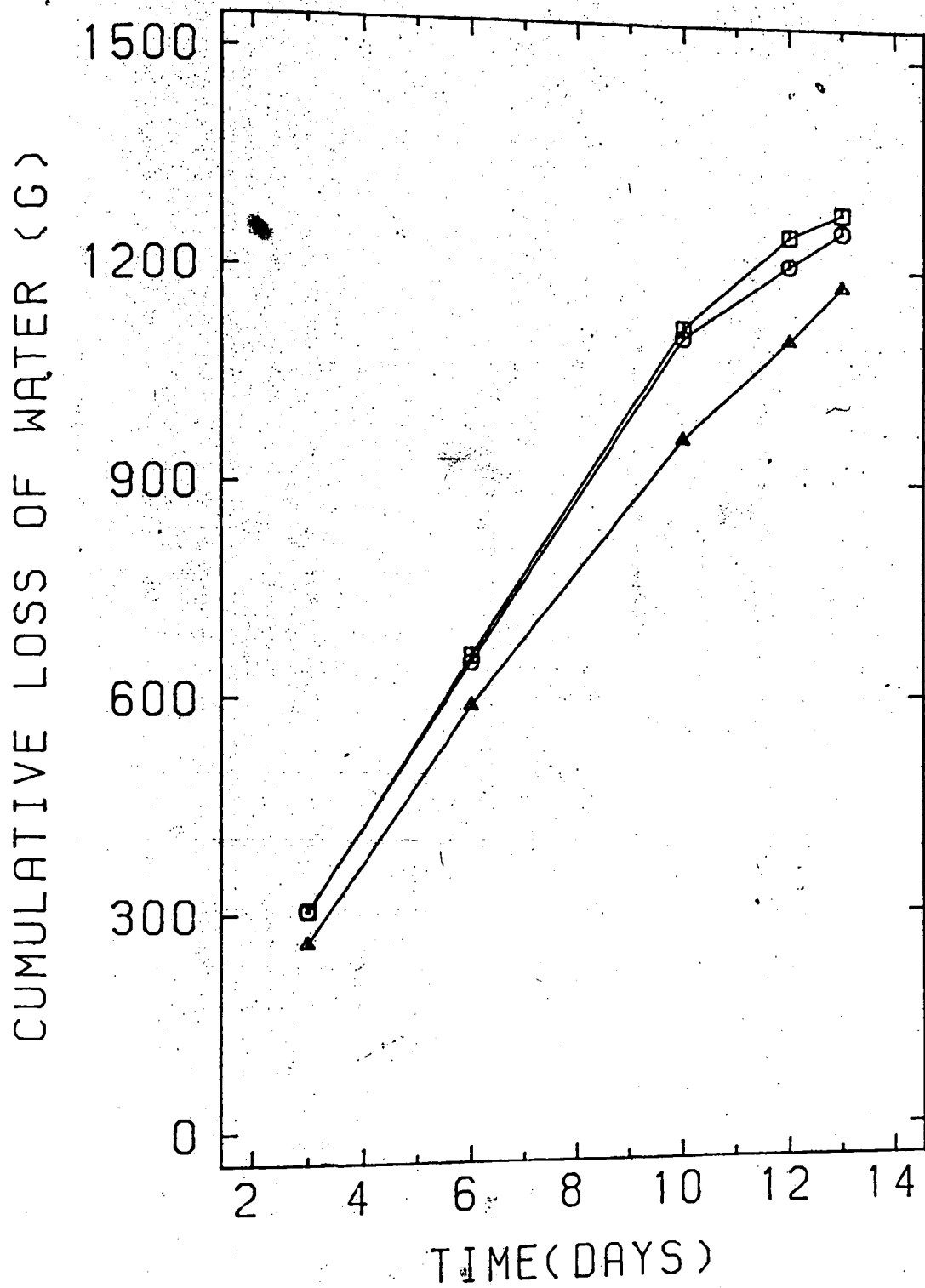
FIG. 8.8. Cumulative weight losses over one drying cycle of pots containing <u>C. monilifera</u> (□), <u>A. longifolia</u> (Δ) or a 1:1 mixture of the two species (0).
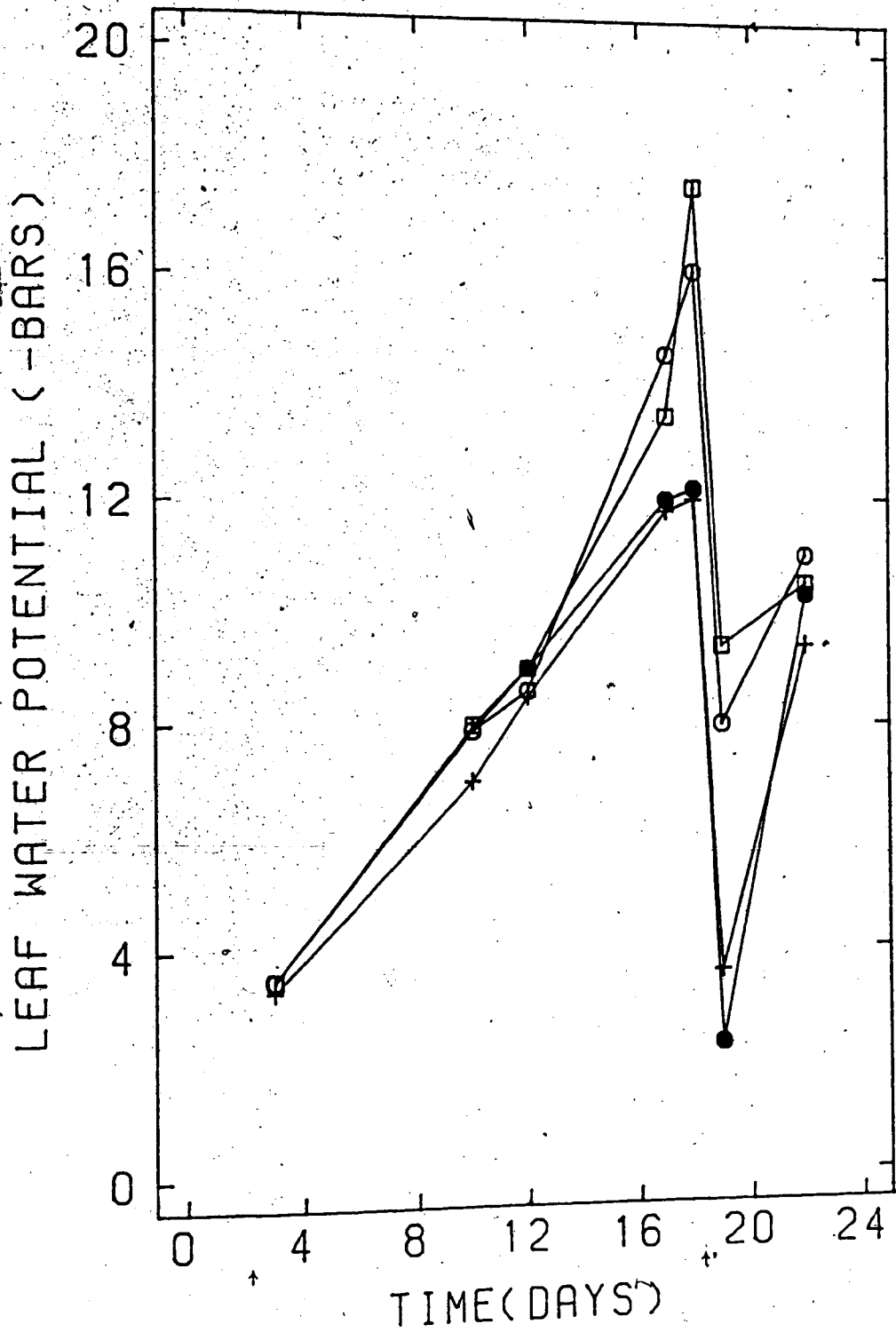
FIG. 8.9. Leaf water potentials over a drying cycle (watered on day 2 and day 18) of C. monilifera in monoculture (□) and a 1:1 mixture (●) and A. longifolia in monoculture (+) and mixture (0).

8.2.4 Discussion

There were up to several days delay after watering in attaining maximum rates of assimilation and transpiration. There was a trend for the maximum rate to decline with successive drying cycles which may have been due to the use of an ageing leaf as well as a new one in measurements.

The more marked drop in transpiration in C. monilifera as stress develops in a drying cycle (Fig. 8.5) is consistent with early stomatal closure which would mitigate against excessive water loss. However, stress (as measured by leaf water potential) developed more rapidly in monocultures of C. monilifera than A. longifolia (Fig. 8.9). It thus appears that A. longifolia is less affected by water stress than C. monilifera which was also apparent from the results in Chapter 7, where A. longifolia suffered less mortality than C. monilifera under prolonged water stress. This behaviour of A. longifolia may perhaps best be described by the term "drought tolerance" (Levitt, Sullivan & Krull 1960). In the field, the better developed root system of C. monilifera would help to delay the development of low water potentials and stress.

8.3 Leaf water potential, osmotic potential and relative water content

8.3.1 Introduction

A relationship between water release curves and drought resistance has been put forward (Weatherly & Slatyer 1957; Connor & Tunstall 1968). Xerophytic species such as A. aneura show a smaller change in water content for a given decrease in water potential than more mesic species (Slatyer 1960). Thus xerophytes generally have a shallower curve of relative water content against water potential than mesophytes. Xerophytes also generally show the highest relative water contents in the field and are more resistant to the induction of water deficits on drying soils since theoretically they can maintain cell turgor in such soils in spite of increasing water potential gradients in the vascular system (Bannister 1971). However, Osmond, Bjorkman & Anderson (1980) point out that water release curves are difficult to interpret because such curves are the product of minute cellular interactions and life form and rooting patterns are also important in drought tolerance. It has also been suggested that xerophytes may show a marked reduction of growth with increasing water stress (Jarvis & Jarvis 1963), so that desiccation

resistance and growth rate may be inversely correlated (Jarvis 1963).

I measured relative water content, leaf water potential and water release curves in C. monilifera and A. longifolia in order to determine if there was a relation between such measurements and the pattern of water use observed in other experiments.

8.3.2 Methods

Monocultures of C. monilifera and A. longifolia were grown in the glasshouse in soil in 25 cm diameter pots and watered at various frequencies so that a range of leaf water potentials developed. The water potentials and relative water content of leaves were measured. Relative water content (RWC) is equivalent to the relative turgidity of Weatherly (1950) and was calculated as follows:

$$RWC\ (\%) = (FW - DW)\ 100/(TW - DW)$$

where FW = fresh weight, TW = turgid weight and DW = oven-dry weight. Turgid weight was obtained after standing detached leaves in holes in a foam sponge filled with distilled water for 24 h in a closed plastic container in a refrigerator. Leaves were blotted dry before weighing.

Pressure volume curves were also obtained by using initially turgid leaves and measuring their weight and corresponding water potential every 5 minutes as they lost water. This enabled a calculation of relative water deficit (RWD) which is the complement of relative water content, (RWD = 100 - RWC), expressed as a %. The reciprocal of leaf water potential was then plotted against RWD. Linear regressions were calculated from the flattened parts of the curves and extrapolated back to zero RWD. Thus the osmotic potential at full turgor could be estimated (from the value on the y-axis) (Scholander, Hammel, Hemmingsen & Bradstreet 1964).

8.3.3 Results

There was a shallower curve of relative water content against water potential in A. longifolia than C. monilifera (Fig. 8.10).

Osmotic potentials at full turgor in C. monilifera and A. longifolia, estimated from the asymptotes in the water release curves, were -0.7 and -1.0 MPa (-7 and -10 bars) respectively, (Fig. 8.11).

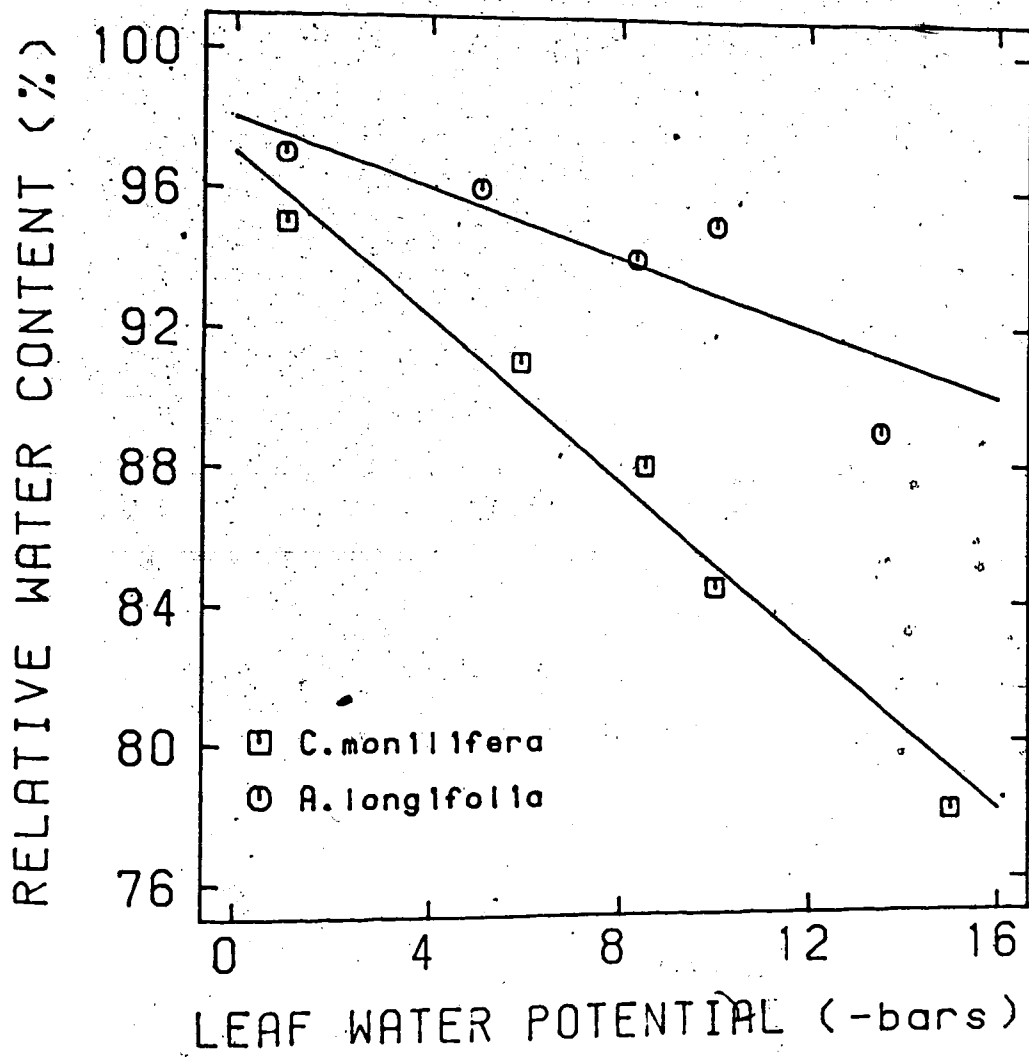FIG. 8.10. Relationship between relative water content and leaf water potential of glasshouse-grown C. monilifera and A. longifolia. Points shown are means of several values.

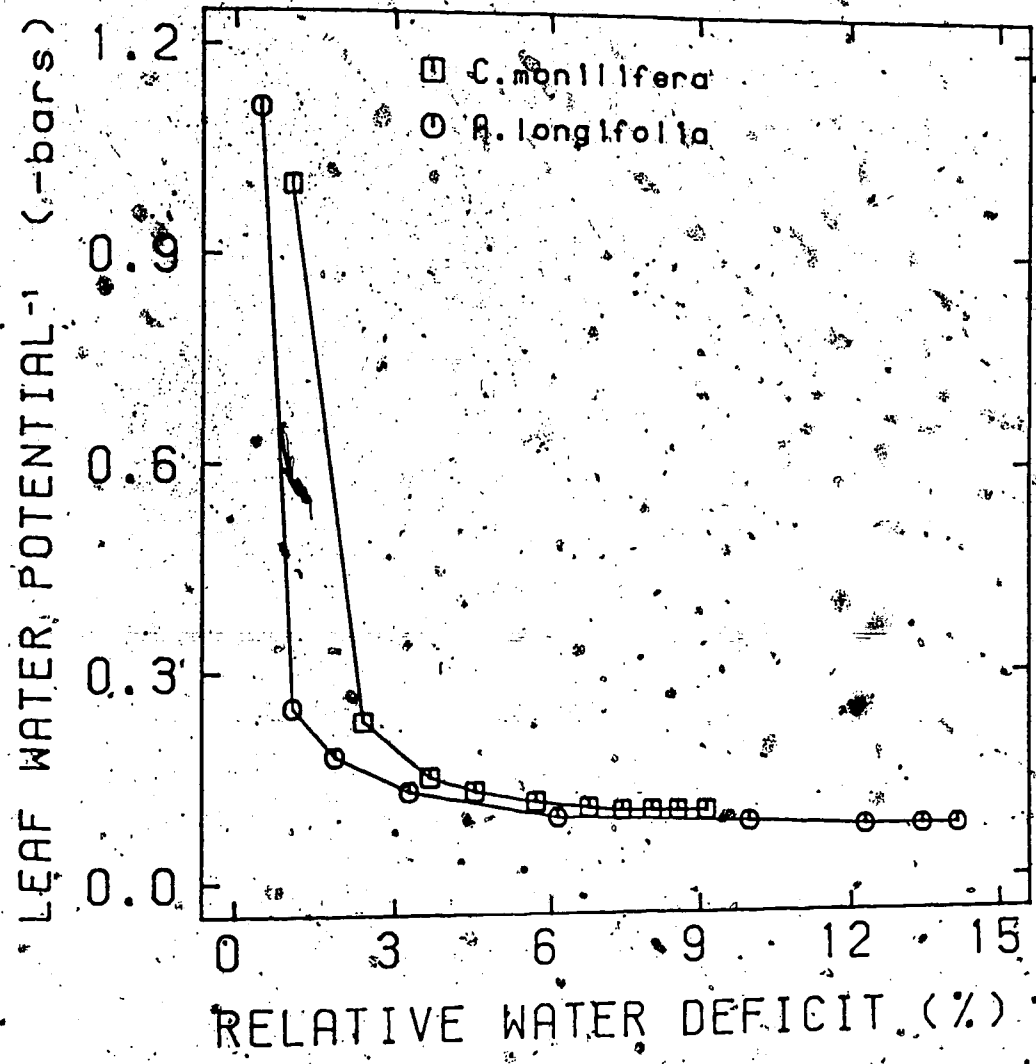FIG. 8.11. Pressure-volume curves of <u>C. monilifera</u> and <u>A. longifolia</u>, showing the reciprocal of leaf water potential against relative water deficit.

8.3.4 Discussion.

The shallower relative water content/leaf water potential relationship in A. longifolia is consistent with this species being more resistant than C. monilifera to the induction of water deficits on drying soils.

The water release curves (Fig. 8.11) do not show a clear linear portion, making it difficult to obtain good estimates of osmotic potential at full turgor. Nevertheless, they are within the range found for mesophytes by Tyree, Cheung, MacGregor & Talbot (1978) but much less than the -6.3 MPa (-63 bars) for Larrea divaricata, a desert xerophyte (Scholander et al. 1964). However, Roberts, Strain & Knoerr (1980) point out that such values may change seasonally.

The leaf water potential of A. longifolia and C. monilifera at a relative water deficit of 10% was approximately -1.6 and -0.6 MPa (-16 and -6 bars) respectively (Fig. 8.10). This would allow A. longifolia to extract water from fairly dry soils without the leaves undergoing a large water deficit. This would allow processes related to turgor such as leaf expansion and growth to still continue (Hsiao 1973).

The higher water potential of C. monilifera above suggests that it may require a moister soil or at least access to moisture deep in the soil or water reserves in the plant to prevent large water deficits, if water is not replenished. If water deficits due to transpiration do occur, however, C. monilifera would tend to be affected before A. longifolia due to its relative inability to maintain cell turgor at low water potentials.

I have observed such behaviour occasionally in the field under dry conditions where growth of A. longifolia has continued while there has been wilting or death of some stems of nearby C. monilifera. These observations and the above results led to investigations of water relations of the study species in the field, described in the next chapter. The above results in patterns of water use help to explain the outcome of competition experiments between the two species in well-watered and water-stress conditions, where the competitive advantage of C. monilifera over A. longifolia was apparent only when well-watered (Chapter 7).

8.4 Summary

The effects of water stress and competition were evident in most of the parameters measured (Table 8.3). A. longifolia withstands water stress better than C. monilifera in monocultures but this ability of A. longifolia is reduced under competition. On the other hand, the success of C. monilifera in competition with A. longifolia when well watered is clear. Such behaviour of the two species provides an example of the statement by Cowan (1981) that "there is a balance between adaptation to withstand drought and other forms of competitiveness, in so far as they are related to rapid growth in the developing seedling".

Table 8.3 Summary of results of glasshouse experiments on water
relations of C.monilifera (C) and A.longifolia (A)

Parameter	Results
Assimilation	The rate in C is lower than in A, but only in monocultures.
Transpiration	When well watered, the rate in C is higher, but under water stress the rate in A is higher.
Transpiration/ assimilation	The ratio is higher in C especially when well watered.
C_i	There is a higher value in C.
Stomatal closure	Closure occurs at c. −0.8 MPa in C and at c. −1.6 MPa in A.
Osmotic potential	The value is slightly higher in C, but values were difficult to estimate.
Leaf water potential	In monocultures, the value is lower in C under water stress, but in mixtures, it is lower in A under stress.

Chapter 9

Water relations of Chrysanthemoides and Acacia
in the field

"Chrysanthemoides monilifera is one of the most plastic and adaptable shrubs in the South African flora. Its unique position in the genus as the only species with a fleshy fruit explains, in some measure, its wide distribution, but its habitat-forms are a problem for physiological research."
(Norlindh 1943)

"As far as one knows, there is nothing fundamentally different about the way in which native Australian species cope with water stress. At the same time, one is aware that native Australian species have not been intensively studied in this respect."
(Cowan 1981)

Introduction

Diurnal and seasonal changes in plant water relations are common in many species (Osmond, Bjorkman & Anderson 1980). Measurement of such changes may be important in explaining the growth and survival of plants especially where water is limiting. The parameters widely used include stomatal conductance, leaf water potential and osmotic potential and soil moisture content. Carbon isotope discrimination ratios are not yet so widely used and relate to CO_2 assimilation as well as transpiration. They are valuable in that they give a long-term integration of physiological parameters.

Stage of tissue development may also play a role in water relations as demonstrated in Ilex opaca (American holly) which grows usually in dry habitats (Roberts, Strain & Knoerr 1980). Young leaves had higher early season initial osmotic potentials than overwintering leaves. I thus investigated water relations in both seedling and mature plants of C. monilifera and A. longifolia in the field in order to determine if such values were similar to those obtained in the glasshouse. I measured stomatal conductance and leaf water potential both seasonally and diurnally and soil moisture and δ^{13} C values seasonally.

9.1 Leaf water potential, transpiration, photosynthesis and soil moisture

9.1.1 Introduction

De Jong (1977) found seasonal variation in leaf water potentials of Atriplex leucophylla growing on coastal sand dunes in California, to be less marked than Williams (1972) found in A. vesicaria in inland Australia. Water potentials of the latter species also varied diurnally, being lowest in the afternoon and recovering by evening (Osmond, Bjorkman & Anderson 1980).

In order to characterise the water relations of C. monilifera and A. longifolia in the field, I measured stomatal conductance and leaf water potential on seedling and mature plants both seasonally and diurnally, as well as seasonal changes in soil moisture. I also measured leaf gas exchange characteristics at one time as a check on the other measurements.

9.1.2 Methods

Stomatal conductance was measured monthly from February 1981 to December 1981, each time c. 2 h after dawn. Diurnal measurements were also made in summer, autumn and winter (February, April and July 1982). There was full sunlight during the April and July measurements but in February, conditions were overcast with high relative humidity (78% to 87%) and rain prevented measurements after 1400 hours. Maximum temperatures during measurement in February, April and July were 22.6°C, 20.5°C and 14.5°C respectively. Readings were made on three intact leaves or phyllodes on seedlings and adults growing near each other in an unburnt area and on seedlings in an adjacent area burnt in spring 1980. A "Delta-T Mk. II" diffusion porometer (Delta-T Devices, Cambridge, England) which measures the rate of water loss from the leaf surface into a dry chamber, as described by Stiles, Monteith & Bull (1970), was used.

Cuticular transpiration rates were assumed to be low and so not considered (Turner, Pederson & Wright 1969). Stomatal conductances, resistances and resultant transpiration figures were calculated from porometer measurements using the units of Cowan (1977, 1981) and the following equation:

$$E = (e'_l - e_a)/Pr$$

where E = transpiration in mmol H_2O m^{-2} s^{-1}

e'_l = saturated vapour pressure in mbars at a particular leaf temperature

e_a = ambient vapour pressure in mbars

P = atmospheric pressure in bars

r = leaf resistance in m^2 s mol^{-1}

The calculation of r was made from the porometer readings taken on both surfaces of the leaves, and then by reference to a calibration curve, made in conjunction with each set of readings and adjusted for temperature. The porometer measures only stomatal and not boundary layer resistance and so transpiration was somewhat overestimated. Leaf temperature was estimated from that shown for the leaf in the porometer chamber. Relative humidity was measured with an Assman hygrometer.

Leaf water potential was measured with the pressure-bomb used in the experiments in Chapter 8. Readings were made on three leaves or phyllodes, removed from the same plants as those used for stomatal

conductance measurements, at dawn each month from February to December 1981 and diurnally in March 1981.

Soil moisture was determined gravimetrically on samples obtained between July 1981 and July 1982. A trench was dug in an open situation each time to minimise the effect of plant roots. Samples were then taken along one side of the trench at depths of 0-10, 10-30, 30-50, 50-70, 70-90 cm. Replicate samples at each depth were placed in air-tight tins. These were weighed, the tins opened and dried at 105°C for 48 h and reweighed. The moisture content was expressed as the loss in weight on drying as a percentage of the oven-dry weight.

Leaf gas exchange measurements were made in June 1982 using apparatus modified for field use by T.D. Sharkey. Readings were made on seedlings and adults of both species in an unburnt area. Three plants in each category were measured and were matched for incident light intensity as closely as possible. Leaves near the top of each plant were used to avoid shading.

9.1.3 Results

Highest seasonal transpiration values are apparent in the warmer months of the year (Fig. 9.1). Seedlings of both species growing in the previously burnt area showed higher transpiration values than did plants in the unburnt area. Generally, there were little differences apparent between the two species in each area. Seasonal climatic details are given in Chapters 2 and 5.

However, differences were more consistent in the diurnal transpiration measurements (Fig. 9.2). Under the overcast summer conditions, transpiration was relatively low. There was also comparatively little change between the 0800 and 1400 hour values. Highest values were consistently obtained from the C. monilifera seedlings growing in the burnt area and lowest from the A. longifolia seedlings in the unburnt area.

In autumn, a peak of transpiration was more evident with highest values generally between 0800 and 1200 hours. Again, highest values were evident in the C. monilifera seedlings in the burnt area, with the lowest in the A. longifolia seedlings and adults in the unburnt area.
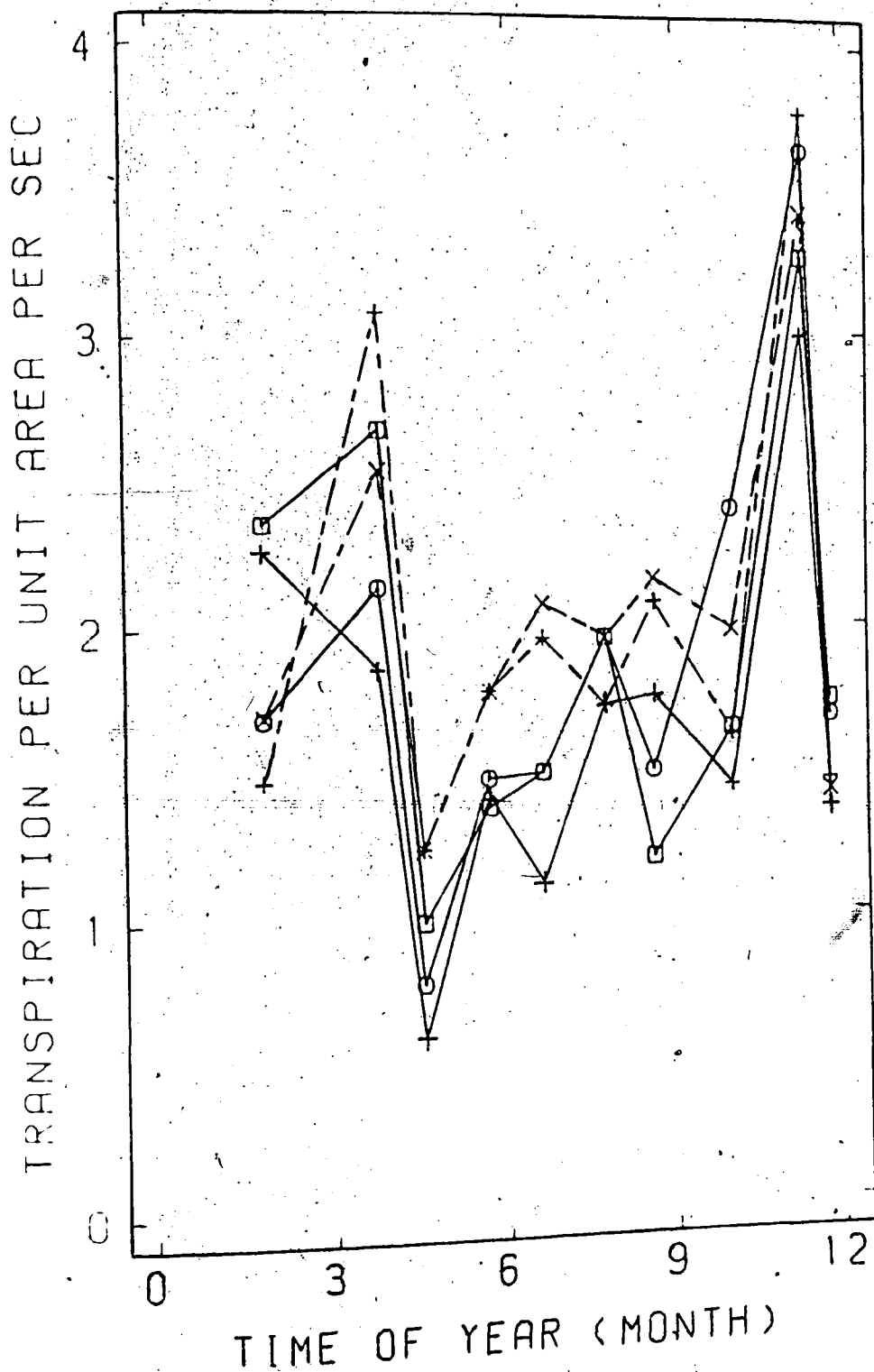
9.1. Transpiration rates (m mol H_2O m^{-2} s^{-1}) measured 2 h after dawn from February to December 1981 of _C. monilifera_ adults (□) and seedlings (+) and _A. longifolia_ adults (0) and seedlings (X). Seedlings in unburnt areas are shown by a solid line and in burnt areas by a dashed line. All adults are in unburnt areas.
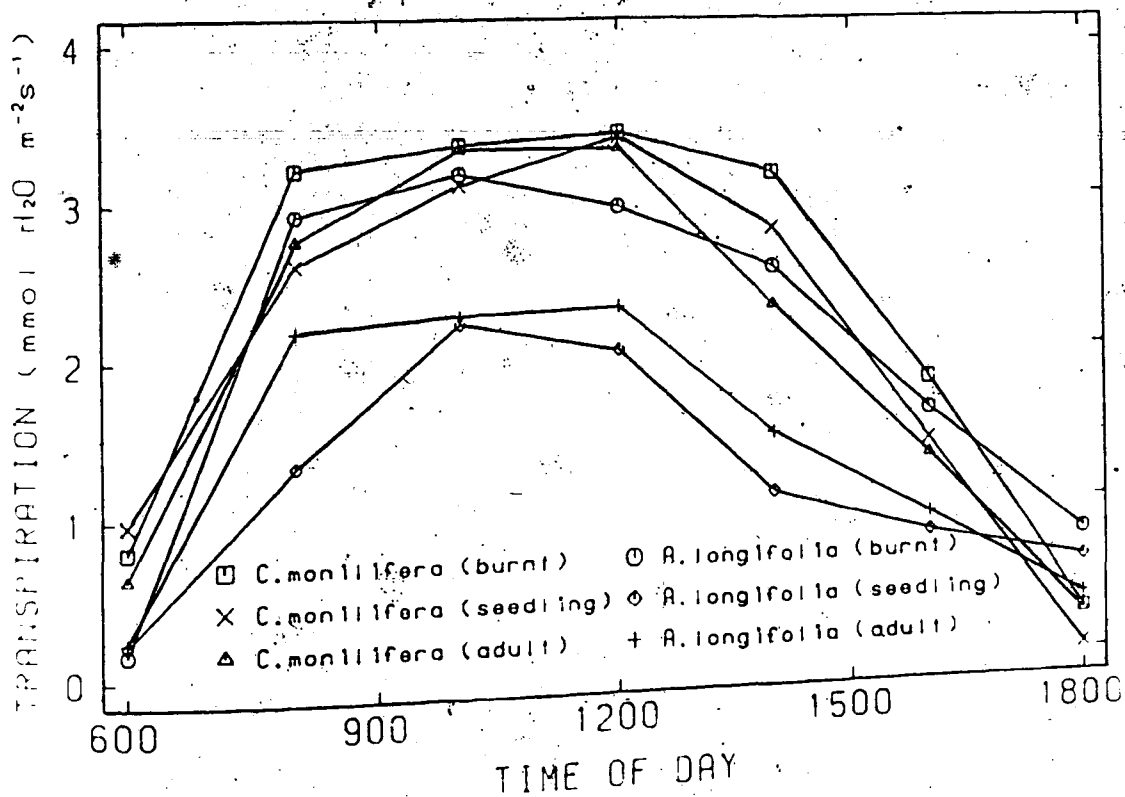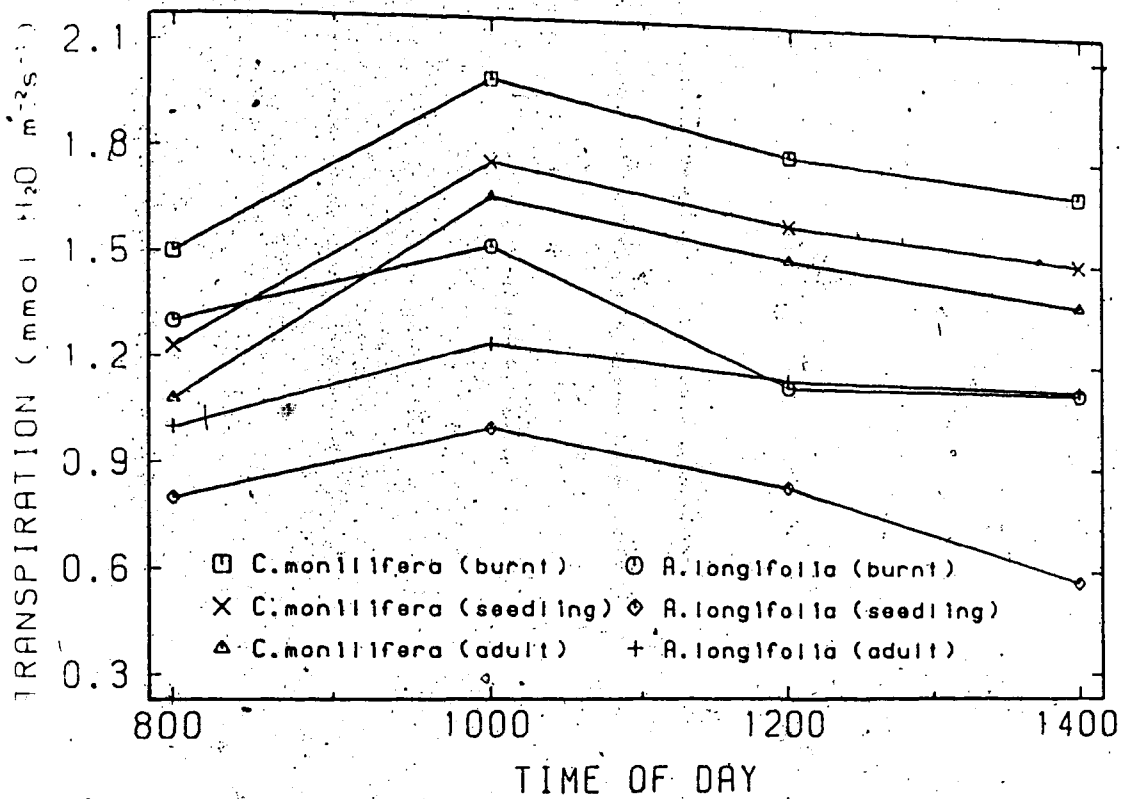
FIG. 9.2 a,b. Diurnal transpiration rates in February 1982 (top) and April 1982 (bottom) of C. monilifera and A. longifolia in unburnt and previously burnt areas.
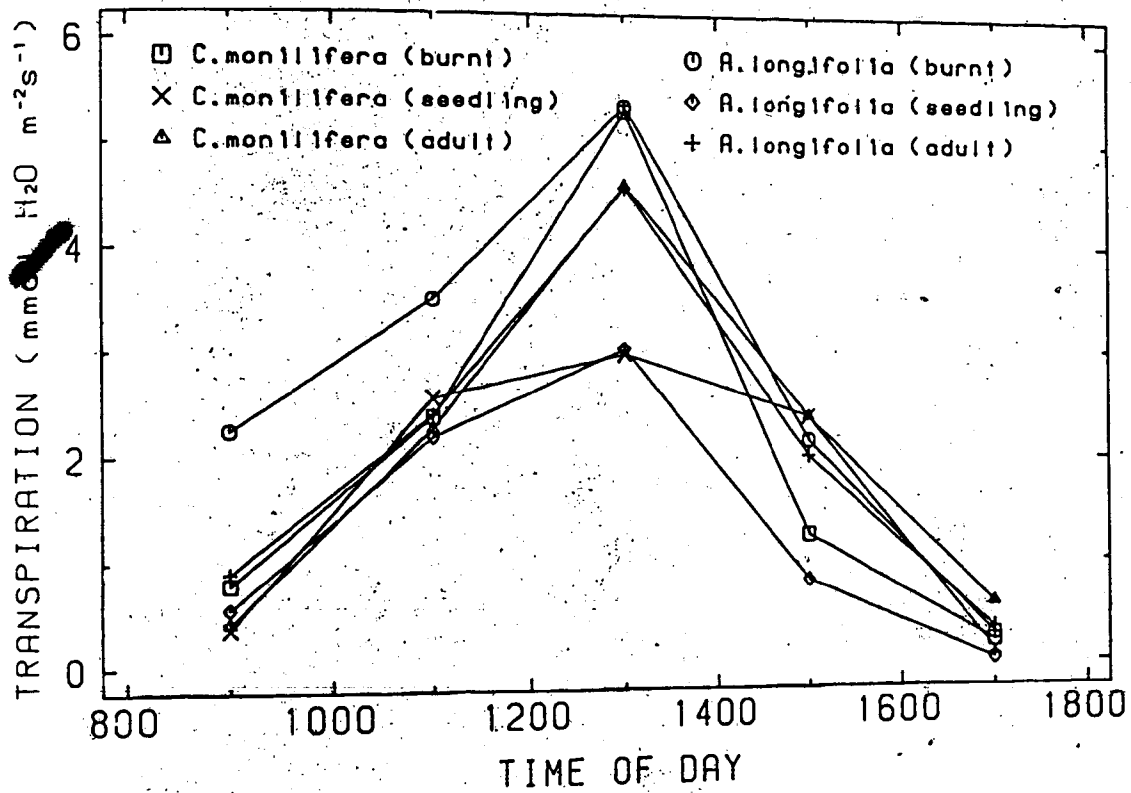
FIG. 9.2 c. Diurnal transpiration rates in July 1982 of C. monilifera and A. longifolia in unburnt and previously burnt areas.
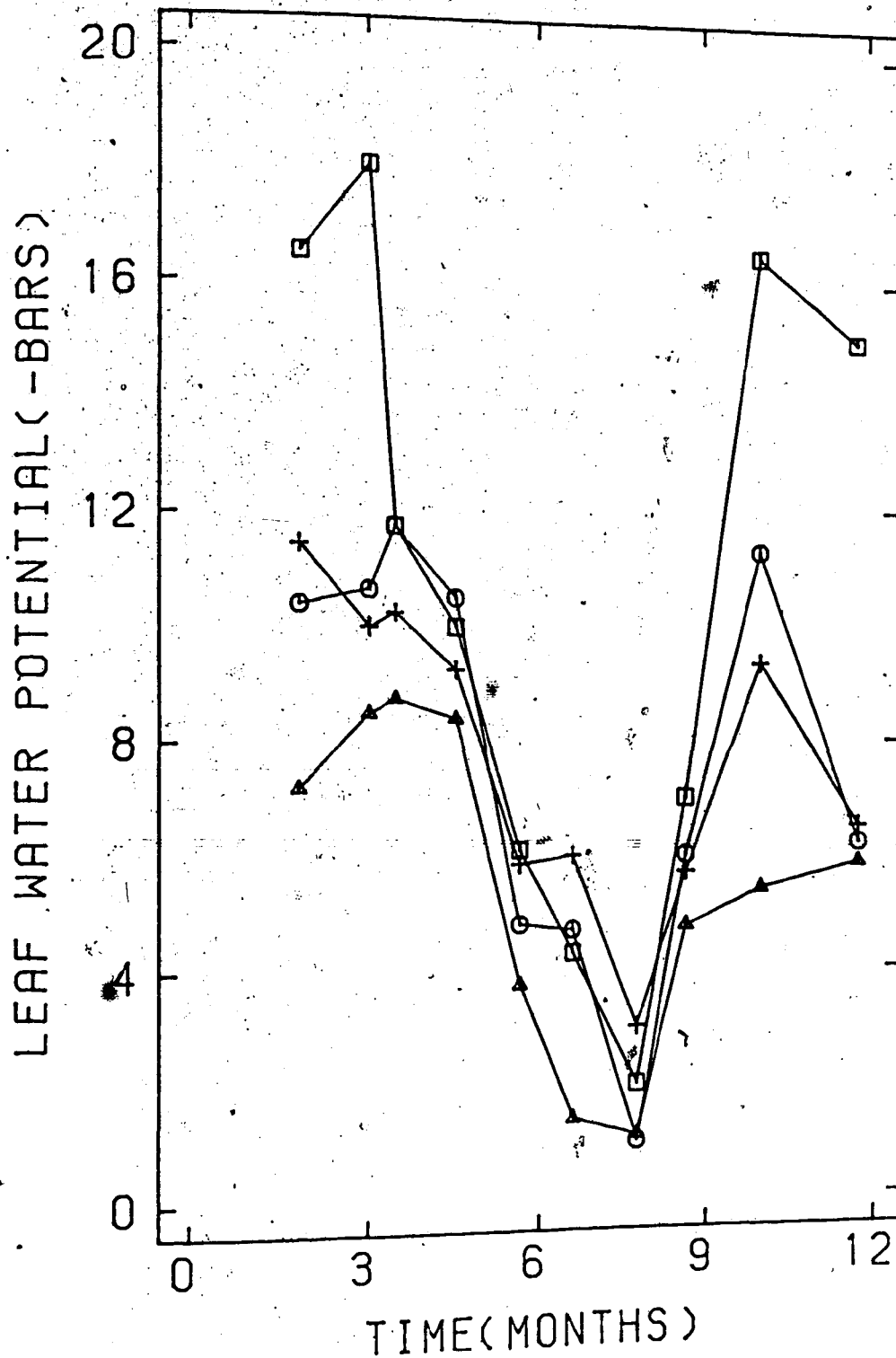
FIG. 9.3. Dawn leaf water potentials from February to December 1981 of _C. monilifera_ (seedlings (Δ) and adults (+)) and _A. longifolia_ (seedlings (□) and adults (0)). All plants were in an unburnt area.
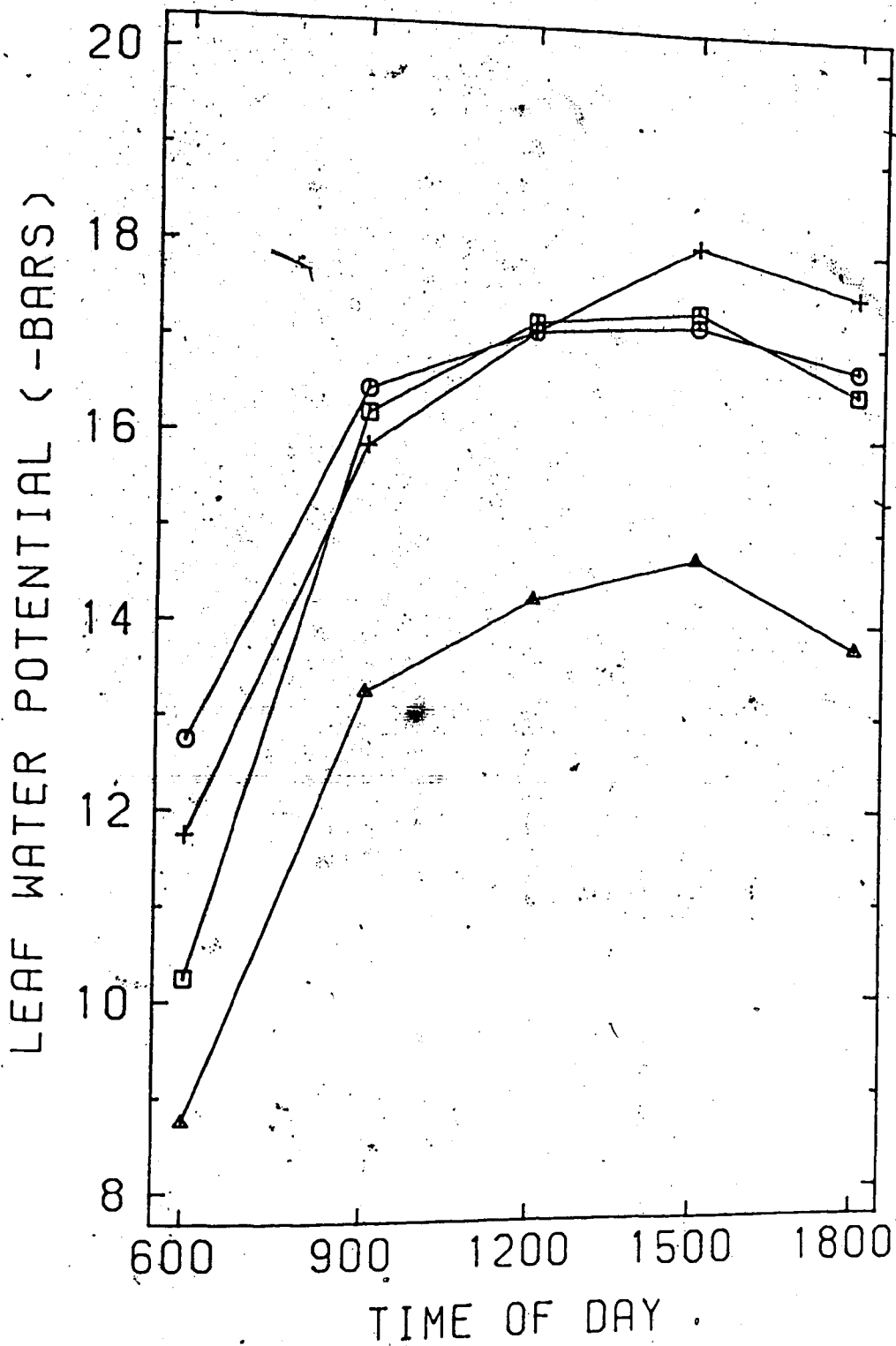
FIG. 9.4. Diurnal measurements of leaf water potential in March 1981 of C. monilifera (seedlings (Δ) and adults (□)) and A. longifolia (seedlings (+) and adults (0)). All plants were in an unburnt area.
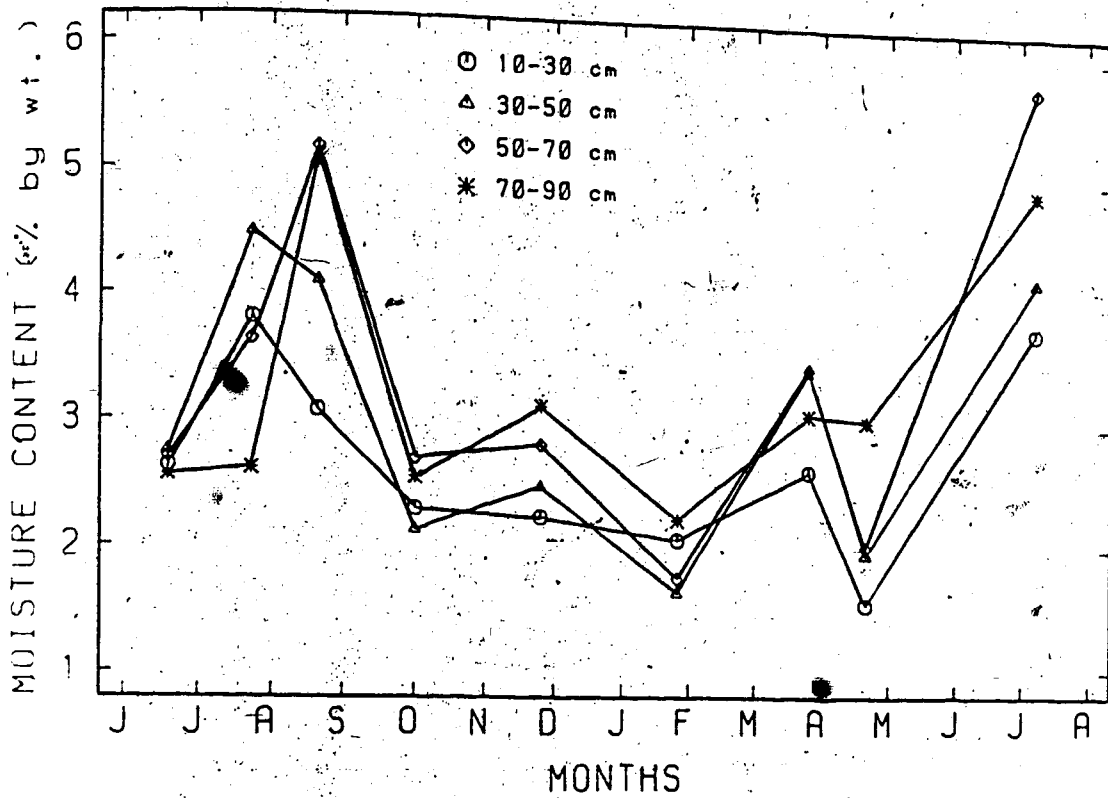
FIG. 9.5. Soil moisture content between July 1981 and July 1982 at four sampling depths. Values at 0 - 10 cm are not included because of the possible influence of shallow-rooted herbs.

Table 9.1 Mean values of assimilation, transpiration, conductance and c_i in adults and seedlings of C. monilifera and A. longifolia at Moruya in June 1982. Standard errors are given in parentheses (n=3)

Species	Assimilation A (μ mol CO_2 $m^{-2} s^{-1}$)	Transpiration E (m mol H_2O $m^{-2} s^{-1}$)	Conductance (mol H_2O $m^{-2} s^{-1}$)	c_i (m bar)	Ratio E/A
Seedlings					
C. monilifera	3.4 (0.6)	1.8 (0.3)	0.09 (0.01)	245 (35)	529
A. longifolia	3.3 (0.7)	1.3 (0.2)	0.06 (0.01)	214 (28)	394
Adults					
C. monilifera	4.6 (0.9)	1.8 (0.3)	0.08 (0.01)	217 (25)	391
A. longifolia	4.5 (1.1)	1.5 (0.3)	0.07 (0.01)	184 (23)	333

In winter, values were surprisingly high, with a marked peak at 1300 hours. Unlike the other seasons, values on either side of this peak dropped away sharply. Values at 0800 hours are not shown but stomatal conductance was negligible at this time, compared with values in summer and autumn. However, 0800 hours was closer to dawn in winter than in the other seasons. Seedlings in the burnt area had the highest values, with again A. longifolia seedlings in the unburnt area generally having the lowest.

Dawn leaf water potentials were highest in winter when soil moisture was also highest and temperatures lowest (Fig. 9.3). In the warmer months, the lowest values were evident in the seedlings of A. longifolia, with little difference between burnt and unburnt areas. On the other hand, seedlings of C. monilifera in an unburnt area had consistently higher values than the other categories. Incomplete measurements were made of C. monilifera seedlings in the burnt area, but where available, higher values were evident than in the unburnt area. Differences between adults of C. monilifera and A. longifolia were small and noconsistent trends were observable throughout the year.

When measured diurnally (Fig. 9.4), leaf water potentials showed the highest values at dawn, fell to their lowest at about 1500 hours, and then rose slowly. Highest values throughout the day were shown by the C. monilifera seedlings. Differences between A. longifolia seedlings and adults and C. monilifera adults were small but seedlings of A. longifolia developed the lowest potentials by the afternoon.

Soil moisture contents were characteristically small for this sandy soil (Fig. 9.5). Fluctuations were obviously related to rainfall but in general values were at their lowest in the warmer months (between October and February), despite December having the highest rainfall. However, a larger proportion of the precipitation would be lost in evaporation in summer. Less evaporation would also be expected from the greater soil depths and in fact the highest soil moisture contents were usually between depths of 50 and 90 cm.

In field gas exchange measurements, there was little difference between the two species in rate of assimilation but rates of transpiration and conductance tended to be higher in C. monilifera (Table 9.1). Differences between adults and seedlings were small.

9.1.4 Discussion

A similar trend was evident in the values of transpiration obtained in the field as those in the glasshouse (Chapter 8). A. longifolia seedlings, at least in an unburnt area, had lower rates of transpiration than did C. monilifera seedlings. A. longifolia adults had generally higher transpiration rates than seedlings but there were no consistent differences between C. monilifera seedlings and adults. Highest transpiration values were shown in the previously burnt area, by C. monilifera and A. longifolia seedlings in autumn and winter and C. monilifera in summer, autumn and winter. This may have been due to a higher soil moisture content in the burnt area because of the covering of ash and the presence of relatively few mature plants.

Since low leaf water potentials are indicative of water stress, A. longifolia seedlings tended to be more stressed than adults or C. monilifera seedlings and adults when measured both seasonally and diurnally. The proximity of C. monilifera may have contributed to these low values in A. longifolia because of competition for water.

Root development and root weight even of isolated seedlings of A. longifolia were less than that of C. monilifera seedlings in the field (Chapter 6). This would place A. longifolia at a disadvantage in not being able to obtain water deeper in the soil and contribute to its low water potentials. These can often result in a reduction or cessation of growth (Jarvis & Jarvis 1963). However, there was little difference between species in assimilation rates measured directly in seedlings (Table 9.1). This may have been a reflection of the higher soil moisture at the time of measurement (in winter). Further such measurements need to be done at various times of the year and incorporate other factors such as dune position, leaf orientation, light and temperature.

A "conservative" strategy is apparent in the growth and water use of A. longifolia especially under field conditions. This would be conducive to fulfilling the need for preservation of its population, particularly of the low density seedlings. It is reflected in the comparatively small, thick, long-lived, high carbohydrate phyllodes of this species (Chapter 6). On the other hand, the larger stomatal conductance and transpiration in C. monilifera may be necessary to assist in cooling the leaves since they are comparatively large, thin, short-lived, with low carbohydrate concentrations (Chapter 6).

9.2 Values of $\delta^{13}C$

9.2.1 Introduction

The carbon isotope discrimination ratio of the total carbon in leaves is expressed as a $\delta^{13}C$ value relative to a standard limestone (Osmond, Valaane, Haslam, Uotila & Roksandic 1981):

$$\delta^{13}C \; (^o/_{oo}) = (\frac{^{13}C/^{12}C \text{ sample}}{^{13}C/^{12}C \text{ standard}} - 1) \; 1000$$

The heavier naturally occurring stable isotope of carbon (^{13}C) is discriminated against during photosynthetic CO_2 fixation. The extent of discrimination is indicated by the $\delta^{13}C$ value; more negative $\delta^{13}C$ values indicate more discrimination. It has been mainly used as an indicator of photosynthetic pathways (Troughton 1979) but, in plants having the C_3 pathway of photosynthesis, it also has the advantage of indicating a long-term integration of intercellular carbon dioxide concentration (C_i). The more negative the $\delta^{13}C$ value, the higher is the C_i value (Farquhar 1980).

Assuming assimilation rate (A) does not increase at the same rate as stomatal conductance (g) and transpiration, and since $C_i = C_a - (1.6 \; A/g)$, high values of g lead to high values of C_i. Thus higher C_i values would be expected to be associated with "water spenders" and lower C_i values with "water savers".

Since factors such as time of the year, stage of development of the plant and dune position with regard to exposure to wind and salt may affect the pattern of water use, I took samples in three different seasons, in sheltered and exposed dune positions, of both seedling and mature plants of C. monilifera and A. longifolia and obtained their $\delta^{13}C$ values, in order to verify the water use behaviour previously found in the two species.

Table 9.2 Values of $\delta^{13}C(\%)$ in C.monilifera and A.longifolia seedlings and adults in exposed and sheltered positions at three sampling times. Standard errors are given in parentheses (n=3)

Species	Season	Seedlings, exposed	Seedlings, exposed & burnt	Adults, exposed	Seedlings, sheltered	Adults, sheltered
C.monilifera	Spring	-29.7(0.4)	-29.9(0.5)	-27.9(0.9)	-30.8(0.5)	-28.3(0.7)
A.longifolia		-26.6(0.5)	-27.0(0.7)	-26.3(0.4)	-29.6(0.3)	-27.4(1.1)
C.monilifera	Summer	-	-29.4(0.7)	-27.0(0.3)	-30.2(0.7)	-28.0(0.9)
A.longifolia		-	-26.3(0.5)	-26.2(0.7)	-29.6(0.5)	-25.0(0.3)
C.monilifera	Winter	-	-28.8(0.6)	-27.6(0.3)	-29.8(0.2)	-27.9(0.3)
A.longifolia		-	-26.1(0.5)	-26.4(0.3)	-28.4(0.5)	-26.8(0.2)

9.2.2 Methods

Five new but fully expanded leaves from the top of three plants of _C. monilifera_ and _A. longifolia_ were obtained in spring (August 1981), summer (February) and winter (July 1982) from each of the following categories:

(a) Seedlings - exposed, fore-dune
(b) Adults   -   "
(c) Seedlings - sheltered, behind fore-dune
(d) Adults   -   "
(e) Seedlings - exposed, burnt fore-dune

Since results from (e) were similar to those from (a) and because very few seedlings of _A. longifolia_ in (a) were present, only (b), (c), (d) and (e) were sampled in summer and winter. All samples were oven-dried, ground finely in a hammer mill and analysed for δ^{13} C values for each plant. These were determined by ratio mass spectrometry, as described by Osmond _et al._(1981).

9.2.3 Results

Values of δ^{13} C for _C. monilifera_ were consistently more negative than for _A. longifolia_ in each category, while sheltered seedlings of both species had the most negative values (Table 9.2).

9.2.4 Discussion

On the basis of gas exchange measurements of glasshouse plants, I concluded in Chapter 8 that _C. monilifera_ was a "water spender" and had a low water use efficiency and low assimilation rate, while _A. longifolia_ was a "water saver" with a high water use efficiency and high assimilation rate. These conclusions appear to be borne out by the results of the δ^{13} C values found in field plants. Thus higher C_i values are indicated in _C. monilifera_ because of its more negative δ^{13} C values (as found in glass-house plants in Chapter 8), which would mean higher conductance and transpiration and/or lower assimilation than in _A. longifolia_.

The highly negative δ^{13} C values and so high C_i values found in sheltered seedlings of both species may be due to these seedlings growing under mature, parent plants and so receiving a comparatively low amount of light. This would mean, in turn, a low assimilation rate and so a high C_i value. Alternatively, in the case of

A. longifolia, since it is likely that seedlings are under water stress because of their low leaf water potentials, their assimilation rate would be depressed, which may lead to higher C_i values.

A further alternative is that the more negative $\delta^{13}C$ values in sheltered plants may be due to their having thinner leaves than those in exposed positions. Such a general correlation has been found when a large number of vascular epiphytes in Australia were examined, although no explanation was offered (Winter, Wallace, Stocker & Roksandic, 1983). However, on an individual species basis, the fern Pyrrosia confluens showed no correlation between $\delta^{13}C$ values and habitat exposure and frond thickness.

9.3 Summary

The field results confirmed the findings of the glasshouse experiments (Chapter 8) in transpiration, stomatal conductance and leaf water potential (Table 9.3).

Table 9.3 Summary of field results on water relations of C.monilifera
(C) and A.longifolia (A)

Parameter	Results
Transpiration	The lowest rate occurs in seedlings of A. The rate is higher in a burnt than in an unburnt area in both species, but particularly in C.
Assimilation	Measurements in winter showed only small differences between C and A.
Stomatal conductance	Conductance is higher in C.
Leaf water potential	Values are highest in seedlings of C and lowest in seedlings of A.
Soil moisture	There is a decrease in the warmer months. There is usually more moisture at 50-90cm than at shallower depths.
$\delta^{13}C$	Values are generally more negative in C. Values are most negative in sheltered seedlings of both species.

Chapter 10

The effect of fire on regeneration
of Chrysanthemoides and Acacia

"If we are in earnest about defending our rich botanical heritage, these plant terrorists will need to be attacked on many separate fronts."
(Hall & Boucher 1977)

"Burning will destroy many seeds and break the dormancy of others, and if the resultant seedlings are destroyed by other methods this will shorten the time required for eradication of the weed."
(Parsons 1973)

10.1 Introduction

After the research program discussed in the preceding chapters, the next logical step was to apply some of the data obtained, in an attempt to control C. monilifera or at least redress the balance between it and A. longifolia. Although this aspect was essentially outside the main thrust of this thesis, a grant from the Coastal Council of New South Wales enabled this investigation to be carried out. An outline is reported here of the results and their relationship to some of the findings given in earlier chapters, particularly in regard to seed dynamics.

The control of C. monilifera in Australia has been attempted on ssp. monilifera by chemical means (Parsons 1973) or a combination of burning and later removal of seedlings by herbicides (Lane 1980, 1981) and on ssp. rotundata by the use of the herbicide, glyphosate (Cooney, Gibbs & Golinski 1982). The use of glyphosate, however, resulted in c. 10% survival of mature plants and prolific regeneration from seedlings.

Burning was investigated as a control measure since high intensity fires, at least, appeared to kill shallowly-buried seeds and so reduce the soil seed pool (Chapter 4). It appeared also that burnt areas provided a more suitable seed-bed for C. monilifera so there should be a better chance of emergence of seedlings from any remaining undamaged seeds which could then be controlled. In another weed of South African origin, Homeria breyniana (Cape tulip), burning promoted corm shooting, the plants being then removed by cultivation or spraying (Pearce 1963). In the case of C. monilifera, reburning of new seedlings may be preferable since cultivation is impractical on the dunes and spraying may be uneconomical or may damage some native species. In addition, since there is a need to supplement the relatively low soil seed pool of A. longifolia (Chapter 3) with sown seed to increase seedling density, such seed sown before a reburn should then receive the stimulus necessary for germination (Chapter 4).

The need for reburning was also evident in the results reported in Chapter 5 where a single burn resulted in 30% of mature plants of C. monilifera resprouting but none of mature A. longifolia. In other weeds, Campbell (1961) reported that repeated burning was necessary

to reduce the vigour of Nassella trichotoma (serrated tussock) on the tablelands of New South Wales. In tropical pastures in Queensland, the practice of controlling Lantana camara (lantana) by burning, sowing Panicum maximum (Guinea grass) and follow-up burning is widespread (Goodchild 1951, Saint-Smith 1964). However, Johnson & Purdie (1981) warn that while burning may result in a reduction in biomass of perennial weeds in the short-term, there may be little if any control in the long term.

Since the effectiveness of fire depends on fire intensity, time of burning, subsequent environmental conditions and physiological state of the plant (Johnson & Purdie 1981), it was decided to compare reburning at different times on control of C. monilifera and seedling emergence of C. monilifera and A. longifolia.

10.2 Methods

An area of c. 1.5 ha was selected at the study site at South Beach, Moruya, running in a north-south direction and centred on the mid-dune and c. 15 m either side of it, where density of C. monilifera was greatest (Chapter 2). Mean densities of mature C. monilifera and A. longifolia were 0.89 and 0.08 plants m^{-2} respectively.

The area was burnt on 9 December 1981 and 24 quadrats, each 15 x 10 m, then located in the burnt area. Reburns were carried out on each of six quadrats on 28 January, 23 March and 25 May 1982 which were 7, 14 and 23 weeks after the first burn. At each reburn, straw was spread over the surface of the six quadrats at a rate equivalent to 1 t ha^{-1} to ensure a satisfactory fire. The final six quadrats were not reburnt and designated as controls.

Prior to the first burn, 100 untreated seeds each of C. monilifera and A. longifolia were sown in 0.5 x 0.5 m sub-quadrats at depths of 0, 0.5, 1.0, 2.0, 4.0, 8.0 cm. At each depth, tiles were placed marked with "Thermochrom" crayons which were used to estimate maximum soil temperatures during the fire. In adjacent areas between quadrats, which were not reburnt, seeds were sown at similar soil depths after the December burn.

Regeneration of mature plants present at burning was monitored in each of the quadrats at approximately monthly intervals until October 1982. Seedling emergence was measured at the same times by counts of plants from sown seeds and from the unsown soil seed pool,
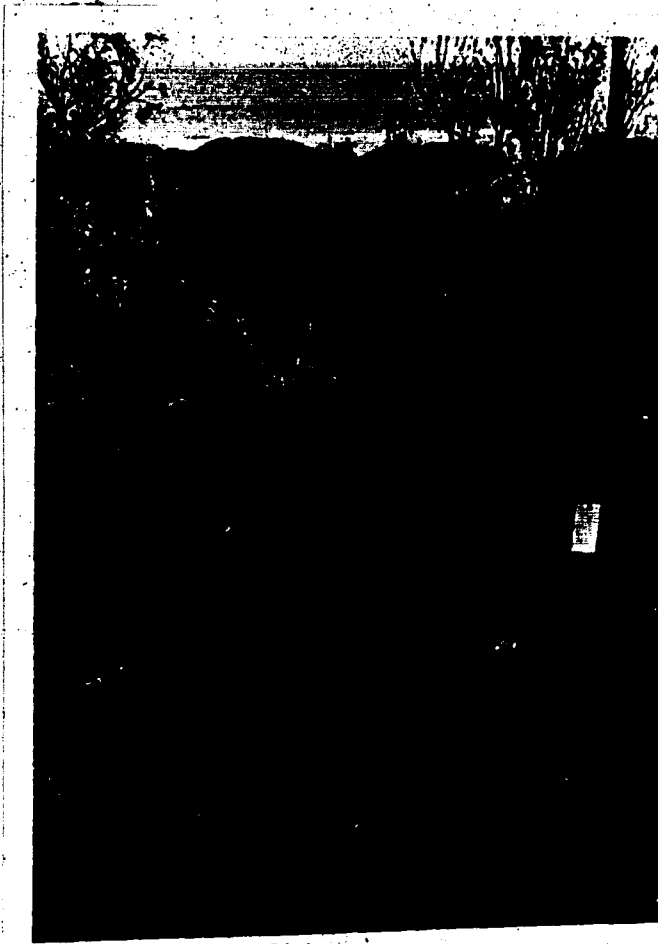
FIG. 10.1. Effect of fire aimed at controlling regeneration of
C. monilifera ssp. rotundata. Foreground shows a plot
on the mid-dune in March 1982 after burning in December
1981 (note regeneration from seedlings and adults);
the middle plot with negligible regrowth was burnt in
December 1981 and January 1982; the unburnt fore-dune
is in the background.

Table 10.1 Densities of mature plants, resprouted plants and seedlings of C. monilifera and A. longifolia after a single burn or reburning 2, 4 or 6 months later (n=6 in each treatment). All figures are numbers m⁻².

Treatment	Date	Mature C. mon.	Resprouted C. mon.	Seedlings of C. mon.	Seedlings of A. long.
Control	Nov 1981	0.84	-	114 **	0.1**
(burnt	Feb 1982	-	0.19	39.8	1.1
December	June 1982	-	0.22	33.2	1.2
1981)	July 1982	-	0.22	35.2	0.9
	Aug 1982	-	0.22	35.7	1.0
	Sept 1982	-	0.22	33.5	1.0
	Oct 1982	-	0.21	35.2	1.0
January	Nov 1981	0.83	-	114 **	0.1**
reburn	Jan 1982	-	0.14	30.3	0.8
	May 1982*	-	0.02	1.4	0.6
	June 1982	-	0.02	1.4	0.8
	July 1982	-	0.02	2.0	0.7
	Aug 1982	-	0.02	2.5	1.1
	Sept 1982	-	0.02	2.5	1.1
	Oct 1982	-	0.02	3.3	0.9
March	Nov 1981	1.06	-	114 **	0.1**
reburn	Feb 1982	-	0.21	45.3	0.9
	Mar 1982	-	0.22	33.8	0.6
	May 1982*	-	0.01	5.0	0.3
	June 1982	-	0.03	5.2	0.4
	July 1982	-	0.03	6.0	0.5
	Aug 1982	-	0.02	5.3	0.7
	Sept 1982	-	0.03	5.7	1.0
	Oct 1982	-	0.03	7.0	1.1
May	Nov 1981	0.81	-	114 **	0.1**
reburn	Feb 1982	-	0.22	86.7	1.7
	May 1982	-	0.22	65.2	1.4
	June 1982*	-	0.01	2.0	0.1
	July 1982	-	0.04	3.9	0.1
	Aug 1982	-	0.05	3.4	0.2
	Sept 1982	-	0.04	3.2	0.2
	Oct 1982	-	0.04	7.9	0.3

* After reburning

** Values obtained from the data in Chapter 2. Means over all treatments are given since quadrats were set out after the December burn.

Table 10.2 Mean number of seedlings per 0.5 x 0.5 m of C. monilifera and A. longifolia present at four times in 1982 from 100 seeds sown at six depths either before or after burning in December 1981. Standard errors are shown in parentheses

Time of sowing	Depth of sowing (cm)	Temperature during burn (°C)	January	February	March	April
					C. monilifera	
Pre-burn	0	225 (25)	0	0	0	0
	0.5	100 (15)	2.2(1.5)	2.0(1.4)	2.0(1.4)	2.2(1.3)
	1.0	75 (10)	9.8(6.6)	4.0(3.0)	4.0(3.0)	4.2(3.0)
	2.0	65 (5)	8.4(6.6)	8.6(6.0)	5.2(4.7)	5.4(4.2)
	4.0	<65	7.0(1.3)	6.0(1.9)	5.8(1.3)	7.2(1.5)
	8.0	<65	16.0(8.2)	10.6(7.9)	7.0(4.4)	7.0(4.2)
Post-burn	0	—	0	0	0	0
	0.5	—	0.8(0.5)	0.4(0.2)	0.2(0.1)	1.6(1.1)
	1.0	—	0	0	1.8(1.3)	3.0(2.0)
	2.0	—	0	0.2(0.1)	0.4(0.2)	3.8(2.6)
	4.0	—	0.2(0.1)	0.2(0.1)	0.4(0.2)	3.8(2.3)
	8.0	—	0	0.2(0.1)	0.2(0.1)	2.4(1.1)
					A. longifolia	
Pre-burn	0	225 (25)	0	0	0	0
	0.5	100 (15)	0	0	0	0
	1.0	75 (10)	0	1.2(0.5)	1.3(0.8)	1.3(0.8)
	2.0	65 (5)	0.2(0.1)	2.0(1.5)	1.6(1.1)	1.6(1.1)
	4.0	<65	0	1.4(0.8)	1.6(1.1)	2.4(1.1)
	8.0	<65	2.4(1.7)	2.4(1.3)	2.0(1.4)	4.4(3.0)
Post-burn	0,0.5	—	0	0	0	0
	1.0	—	0	0	0	2.8(2.3)
	2.0	—	0	0	0	1.4(0.9)
	4.0	—	0	0	0	3.8(2.6)
	8.0	—	0	0	0.6(0.3)	13.4(5.3)

the latter by counting and marking seedlings in six permanently located areas, 2.0 x 0.5 m, evenly spaced in each quadrat.

10.3 Results

The December burn caused 100% mortality of mature A. longifolia. However, resprouting of 26% of C. monilifera occurred by June 1982, either from the base of plants or along the layered stems (Table 10.1, Fig. 10.1). Some had flowered and set seed by this time. Reburning resulted in only 2, 3 and 5% of the number of plants in November 1981 resprouting after the January, March and May 1982 reburns respectively (Table 10.1, Fig. 10.1). These appeared to be associated mostly with areas of lower fire intensity near the edges of the quadrats but also some resprouts survived the May burn.

There were very few seedlings of A. longifolia before burning but their density increased by up to a mean of 13 times after burning (Table 10.1). On the other hand, the density of C. monilifera seedlings decreased to a mean of 44% of the November levels after the December burn and to 5% after reburning. The January and March burns killed all seedlings but some (<5%) survived the May burn and are included in the total numbers in Table 10.1. However, the ratio of C. monilifera to A. longifolia seedlings still varied from 4:1 to 24:1.

In the sown seed sub-quadrats, seedlings in general emerged faster from the pre-December burn sowing (Table 10.2). From post-burn sowings, C. monilifera seedlings emerged before those of A. longifolia. There were no significant differences (ANOVA, $P > 0.05$) in the number of seedlings of C. monilifera which emerged from depths between 1 and 8 cm but emergence of A. longifolia was best from 8 cm (Table 10.2). Where densities of A. longifolia were highest (from 8 cm), grazing by kangaroos (Macropus giganteus) was also evident.

10.4 Discussion and summary

The short intervals between the first and second burns (from 2-6 months) in this experiment provided a severe test of the regenerative potential of C. monilifera. Most practical considerations would preclude the spreading of straw and a longer interval would be necessary to allow accumulation of plant material to carry a second burn. However, in view of seeds being again produced within 6 months of the first burn, this would appear to set an upper limit to the

intervening period if fire were to be used as the sole control measure. Also regrowth was larger and harder to kill if the period between burns was extended to 6 months. Aside from such problems, the result of reburning in limiting regeneration from resprouting to 5% of the plants was encouraging.

However, even after double burning, C. monilifera seedlings were present in densities of up to 8 plants m^{-2}, which still present a control problem. The reason for this regeneration may have been that most seedlings from the natural seed pool came from a depth of 1-2 cm, as estimated by the length of the hypocotyl in 100 seedlings. Seeds at such a depth would be unlikely to be affected by the control burns which were of comparatively low intensity. This is borne out by the similar final results in seedling numbers from seeds of C. monilifera sown before or after the December burn (Table 10.2). Most seedlings of A. longifolia emerged from a depth of at least 2 cm from the natural soil seed pool, estimated to be 13 viable seeds m^{-2} (Chapter 3). There was therefore an emergence of only c. 10% which was probably due to the other seeds being unaffected by the low intensity fires. There was poor emergence of sown seeds of A. longifolia from 0-4 cm. It may be that a combination of weathering and heating promotes better germination in A. longifolia, especially since Aveyard (1968) found heating of the seed with sand at 105°C for 10 min increased germination of untreated seed from 14% to only 32%.

Possibly a combination of herbicides and burning would be a more effective and feasible method of control. A herbicide could be used in spring, followed by burning in summer or autumn. The fire intensity should be increased by dead leaves from the herbicide treatment, leading to better control of mature plants and better regeneration of native species such as A. longifolia. I have observed less resprouting of mature C. monilifera after high intensity fires where there has been dense grass cover under the plants. In order to control seedling regeneration, the herbicide-burning treatment would probably have to be repeated after 12 months.

Chapter 11

Synthesis

"... we have much less insight into the strategies of the system in accepting or rejecting the exotic. As regards two systems only do we have any extensive knowledge of this, and these are man's imperfect systems in which the exotic is often seen and recognised as a pest or a weed, something which is undesirable and which is controlled or eradicated by the use of energy-rich devices such as pesticides or herbicides."
(Weir 1977)

LOSSES OF CHRYSANTHEMOIDES AND ACACIA
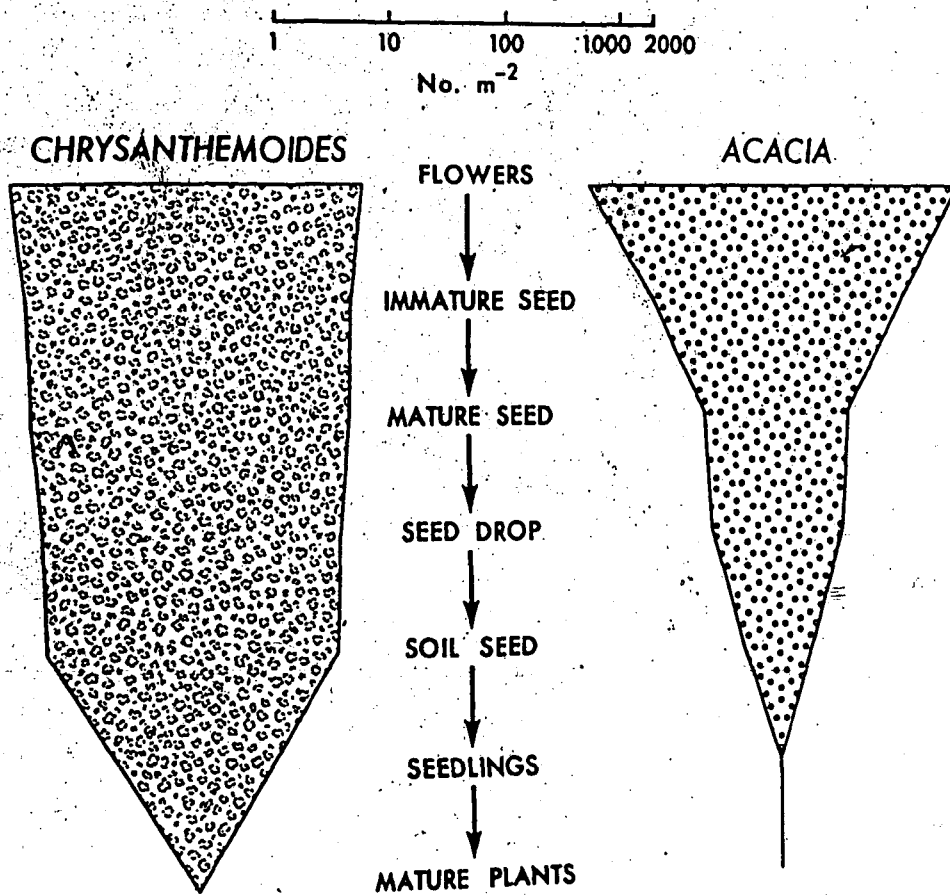## BETWEEN DEVELOPMENTAL STAGES IN AUSTRALIA

FIG. 11.1. Diagrammatic summary of losses of Chrysanthemoides and Acacia between developmental stages in Australia.

It is important in understanding why an invasive species is successful to look also at the species being displaced. Hence in this study in disturbed coastal communities, I investigated the behaviour of C. monilifera, as well as that of the previous dominant, A. longifolia.

11.1 Reasons for success of Chrysanthemoides in Australia

It was established in Chapter 2 that C. monilifera was invasive in Australia at the study sites since it appeared to be actively displacing A. longifolia from its existing niche in the ecosystem. Growth and development of mature A. longifolia were less in invaded areas, particularly on the fore-dune, but there was no evidence of mortality of mature plants due to C. monilifera. It appeared that damage and so stress due to predators was a more important factor in this regard.

Work reported in other chapters has shown that C. monilifera is successful in all of the critical stages for an invasive species (Fig. 11.1):

1. Seed production;

2. Seed longevity and seed pool;

3. Seed germination and seedling emergence;

4. Seedling establishment;

5. Growth to maturity.

11.1.1 Seed production

C. monilifera had a long flowering period (autumn to spring) and a yearly production in Australia of over 4000 seeds m^{-2}. This apparently wasteful investment in reproduction may be useful in coping with predation by birds, which in some months was high. Although not investigated, high seed numbers could also have attracted birds, and so increased bird populations in invaded areas. High fecundity also

helps to ensure that seeds are distributed not only to "safe" sites (Sagar & Harper 1961) where there is opportunity for establishment, but also beyond the invaded area to initiate new invasions. As well, it helps to maintain genetic diversity in the population and to increase the probability that appropriate genotypes occupy safe or new sites (Williams 1975).

By contrast, the flowering of A. longifolia was restricted to spring and in Australia only c. 100 seeds m^{-2} were produced. There was little reduction in seed production of A. longifolia near mature C. monilifera (Chapter 7). It appeared that yearly variation was due more to rainfall, since seed numbers of A. longifolia were markedly reduced in a dry year (Chapter 3). The high rates of seed predation of A. longifolia in Australia do not occur in Acacias in South Africa where seed production is high and more akin to that of a ruderal.

11.1.2 Seed longevity and seed pool

Longevity of seed of C. monilifera was not as great as that of A. longifolia. After 2 years burial at various depths, there remained a mean of 2% and 6% viable seeds of the original total of C. monilifera and A. longifolia respectively. There was a larger number of predated or missing seeds in the case of A. longifolia.

On the other hand, the greater fecundity of C. monilifera led to more than 60 times more viable seeds in the soil of C. monilifera than of A. longifolia (Chapter 3).

11.1.3 Seed germination and seedling emergence

C. monilifera has less innate seed dormancy than A. longifolia so that, in established stands, there were c. 500 times more seedlings of C. monilifera. This resulted in a swamping of populations of A. longifolia by those of C. monilifera once the latter became established in the vicinity. As well, seedlings of C. monilifera emerged faster than those of A. longifolia at low soil water potentials.

A. longifolia can be regarded as having a "bet-hedging" strategy in that, in the absence of fire, only a small fraction of the seed pool is in a germinable state and so there is only a trickle of seedling emergence.

11.1.4 Seedling establishment

Pot experiments at high densities showed that C. monilifera outcompeted A. longifolia when well-watered. At low soil water potentials, A. longifolia seedlings in monocultures survived better than those of C. monilifera, but in mixtures it was demonstrated that C. monilifera could prevent survival of A. longifolia (Chapter 7).

In the field, when seedlings were established at high densities under good growing conditions (after fire), C. monilifera again outcompeted A. longifolia. Under more normal conditions of lower densities in unburnt areas, percentage mortality of seedlings of C. monilifera was slightly greater than that of A. longifolia, due partly to a density-dependent effect in C. monilifera. Another reason was that A. longifolia had a greater resistance to water stress which involved an efficient water use but low growth rate.

Seedling mortality in C. monilifera was compensated by comparatively high numbers. Total numbers did not fluctuate widely since there was a high turn-over rate, with seed and seedling populations being more or less continually replenished (Chapter 5). In unburnt areas, the seedling banks may be classed as "persistent" because of the relatively slow individual growth and development rates.

In growth physiology, C. monilifera seedlings had the lower assimilation rate per unit leaf area in the laboratory but had a greater leaf area ratio and a greater relative growth rate than A. longifolia.

C. monilifera was characterised as being a "water-spender" (Chapters 8, 9). Because of the wide fluctuations in monthly rainfall and soil-water availability, this behaviour would not be conducive to survival in times of water stress. Since there were comparatively high seedling densities in established stands, where the soil seed pool had built up sufficiently, the available moisture per plant in a given area would often be low.

The water use behaviour of C. monilifera would deplete soil moisture and so leave less available to seedlings of A. longifolia. It would also be conducive to leaf area production and so produce more shade under plants. This "shading" strategy would assist in the competitive efficiency of C. monilifera by reducing the light intensity received by other species. This is likely to be important

in the success of invasive species generally, as occurs for example with __Pittosporum__ __undulatum__ (sweet pittosporum) (Gleadow & Ashton 1981). Root competition and interaction between root and shoot competition can however also be important (Chapter 7).

A shading strategy may also help to provide a "regeneration niche" (Grubb 1977) under the canopy of C. monilifera. This is necessary to support a bank of persistent seedlings and so ensure the survival of succeeding generations. The micro-environment created underneath mature plants depends on shading by the plant as well as on protection from wind and sand blast and on litter fall. Litter may provide nutrients for the seedlings as well as preventing excessively high temperatures and drying out of the soil.

11.1.5 Growth to maturity

In unburnt areas, the study was insufficiently long to compare growth to maturity of the two species. Seedlings which emerged in such areas at the beginning of the 3-year study had not flowered by the end of it.

In burnt areas, however, some resprouted plants of C. monilifera reached maturity within 6 months and some seedlings within 12 months.

11.2 Disturbance

The only disturbance specifically studied in relation to the above critical stages in success was that of fire. However fire had a major effect on regenerative strategies and growth of both species. Adult plants of A. longifolia were killed by fire but 26% of adult C. monilifera resprouted. It appears that fire breaks the dormancy of buds at the base of the plant and along prostrate stems.

After a fire, the seed bank of C. monilifera near the soil surface was reduced proportionately more than that of A. longifolia. However, sufficient seeds of the former still remained for subsequent C. monilifera seedlings to outnumber those of A. longifolia by some 20 times. The seedling banks of both species become fast-growing rather than persistent ones, probably because of the enhanced post-fire resources. This is in contrast to some other coastal species in N.S.W. such as Banksia spp. emerging after fire whose growth rate is still comparatively low (Siddiqi, Myerscough & Carolin 1976). Germination and growth in an ash-bed were still greater in C. monilifera than in A. longifolia under the conditions observed.

It is interesting to speculate on the change from the previous bet-hedging strategy of A. longifolia to that after fire, as demonstrated by the greatly increased germination of its seed pool. It is probably linked to more available nutrients, less competition and better moisture and temperature conditions in the seed-bed. It may also be linked to lower levels of soil-borne pathogens. Although not reported in this thesis, Fusarium spp. were isolated from seedlings in unburnt areas, particularly those showing some evidence of general debility.

In burnt uninvaded areas, the mature population of A. longifolia is usually replenished successfully, since resources are improved and stress reduced, with less competition from mature plants. Fire in such areas is important in Acacia regeneration since mature plants are comparatively short-lived.

The post-fire strategy of A. longifolia becomes less efficient if an invading species such as C. monilifera, in the form not only of seedlings but also resprouts from mature plants, competes for the extra resources.

The ecological differences between ssp. monilifera and rotundata in their response to fire may partly explain their distribution in Australia. Fires on coastal dunes are likely to be of lower intensity and less frequent because of more sparse vegetation and lower fuel loads than those in inland forested areas. Thus conditions are conducive to invasion of coastal dunes by ssp. rotundata since fire is not needed for its germination and will even reduce the numbers of shallowly-buried seeds. On the other hand, ssp. monilifera appears more suited to forested areas since fire stimulates its germination and the population can be replenished even if adult plants are killed. Further, high intensity fires are more likely to stimulate germination of deeply buried seeds of ssp. monilifera.

11.3 Summary

The degree of success of C. monilifera in Australia in each of the critical stages studied makes it difficult to identify any weaknesses in its life cycle which could be exploited in possible control measures.

The real advantage of C. monilifera over A. longifolia in Australia is a numerical one, as exemplified by the results from seed output and seed germinability. This is probably due to the

comparative freedom of C. monilifera from predators, especially in the reproductive phase which points to the need for control measures to concentrate on this phase.

11.4 Future research

If localities could be found in South Africa where the two species studied co-exist, as appears likely at Port Elizabeth (Fig. 1.5), similar measurements to those in Chapter 2 would answer the question whether a mirror image of the situation in Australia was occurring in South Africa. If leaf area per plant was increased in the absence of predators, the demonstrated assimilation rate and so growth potential of A. longifolia makes this appear likely. It would also be of value to conduct field experiments in South Africa, such as studies of interactions between Chrysanthemoides and Acacia, similar to those reported here in Australia so that the results in the two countries could be compared. It may then be possible to discern some common factor in the success of invasive species generally.

There is a need to determine whether both A. longifolia var. longifolia and var. sophorae are present in South Africa. Although not reported in this thesis, I found no differences in rates per unit leaf area of assimilation, transpiration and conductance in seedlings of both varieties. However, no ecological comparisons were made between the two varieties which would be necessary to complement the physiological investigations before the results reported in this thesis were used to assist in any program of control of A. longifolia in South Africa.

Further research is also needed on control measures for invasive species in natural plant communities. The use of a combination of fire and herbicides may be of value in this regard for control of Chrysanthemoides in Australia, but it has not yet been tested in coastal communities in N.S.W. Results on ssp. monilifera in Victoria have been promising. It should be possible to utilise a seed and seedling dynamics model of C. monilifera, as outlined in Chapter 3, to give an indication of the best time to implement such measures and of the expected number of seeds and seedlings if adult plants were killed. Fire may also be useful for control of Acacia in South Africa, by killing mature plants and stimulating emergence of seedlings which may then be controlled by a selective herbicide.

There appears to be potential also for biological control both of
C. monilifera in Australia (Weiss 1981 b; Morris 1982) and
A. longifolia in South Africa (S. Neser, personal communication).
However there is a need for research on genetic variation in both
species which may also indicate the number of introductions of the
plant into a country (Marshall & Weiss 1982). The smaller the amount
of genetic variation, the better are the chances for successful
biological control (Burdon, Marshall & Groves 1981). There is a need
also for further research on the ecological behaviour of C. monilifera
in South Africa which information is likely to be important in the
success of any biological control program in Australia (Wapshere
1973).

In Australia, C. monilifera ssp. monilifera apparently serves no
useful purpose in forested or other areas but ssp. rotundata is useful
in stabilisation of sand dunes and recently mined areas. For this
reason, measures aimed at control of ssp. rotundata should take into
account the need for stabilisation until an alternative species such
as A. longifolia can be established and take the place of
C. monilifera. It would seem preferable, therefore, if a biological
control program was attempted, to concentrate on organisms which
attack only the seed production phase of C. monilifera, such as
tephritid flies (Mesoclanis spp.). In this way, plants would not be
killed in the short-term but further increases in density and spread
to new areas would be checked by reducing output from the seed
production phase.

In view of the already widespread distribution of both
sub-species of C. monilifera in Australia, it is probably too late to
eradicate them. However, some form of containment is necessary since
they are likely to spread further in Australia, as A. longifolia and
other Australian species have done in South Africa. A. longifolia has
invaded native communities in South Africa over a period of 150 years
while wide-spread planting of C. monilifera ssp. rotundata was
commenced only up to 35 years ago in Australia. While control of
C. monilifera in Australia by biological means appears practicable,
other practical considerations preclude it at the present time.
Therefore, in the interim period, other measures need to be
implemented. These should take into account the composition of the
native community and ideally be able to utilise it to help in the
containment of C. monilifera. Certainly some coordinated action
between the relevant organizations needs to be taken. As pointed out
by Wallis (1980), "any attempted solution to the introduced
animal/plant problem must focus on man in terms of his introducing the

species in the first place, his encouragement of its spreading by habitat modification and how he is likely to react to different management proposals."

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Appendix 1

Analysis of soluble sugars and non-structural carbohydrates
(Method of S.C. Wong)

Glucose

Approximately 10 mg of ground material was used in the assay.
Sugars were extracted in boiling water for 15 min and analyzed using
enzymatic methods. Free glucose plus fructose were measured from the
leaf extract using a glucose specific assay (Calbiochem-Behring
Glucose s.v.r. no. 870104), after converting fructose to glucose with
phosphoglucoisomerase (Sigma P-5381). Glucose was converted to
glucose-6-phosphate in the presence of hexokinase, and then oxidised
to 6-phosphogluconate by glucose-6-phosphate dehydrogenase, reducing a
molar equivalent of NADP. Sucrose was hydrolysed by incubating the
leaf extract at 37°C for 2 h in a water bath with invertase (Sigma
I-5875) in 0.1 N acetate buffer (pH 4.6). The change in absorbance at
340 nm is proportional to the glucose concentration in the range from
0 to 10 ng ml^{-1}, and was measured with a Varian 634 spectrophotometer.
The assay was done at room temperature and was initiated by an aliquot
from the sample and finished when no more change in absorbance
occurred.

Starch

Starch content was obtained by incubating the leaf extract at
37°C for 48 h in a water bath with 0.5% "Clarase 900" (Miles
Laboratories) in 0.1 N acetate buffer (pH 4.6). "Clarase 900" is a
mixture of several digestive enzymes which hydrolyze starch and
sucrose to hexoses. Starch was obtained by subtracting the glucose
plus fructose fraction from total glucose assayed in the "Clarase"
digest.

Appendix 1

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(Method of S.C. Wong)

Glucose

Approximately 10 mg of ground material was used in the assay. Sugars were extracted in boiling water for 15 min and analyzed using enzymatic methods. Free glucose plus fructose were measured from the leaf extract using a glucose specific assay (Calbiochem-Behring Glucose s.v.r. no. 870104), after converting fructose to glucose with phosphoglucoisomerase (Sigma P-5381). Glucose was converted to glucose-6-phosphate in the presence of hexokinase, and then oxidised to 6-phosphogluconate by glucose-6-phosphate dehydrogenase, reducing a molar equivalent of NADP. Sucrose was hydrolysed by incubating the leaf extract at 37°C for 2 h in a water bath with invertase (Sigma I-5875) in 0.1 N acetate buffer (pH 4.6). The change in absorbance at 340 nm is proportional to the glucose concentration in the range from 0 to 10 ng ml^{-1}, and was measured with a Varian 634 spectrophotometer. The assay was done at room temperature and was initiated by an aliquot from the sample and finished when no more change in absorbance occurred.

Starch

Starch content was obtained by incubating the leaf extract at 37°C for 48 h in a water bath with 0.5% "Clarase 900" (Miles Laboratories) in 0.1 N acetate buffer (pH 4.6). "Clarase 900" is a mixture of several digestive enzymes which hydrolyze starch and sucrose to hexoses. Starch was obtained by subtracting the glucose plus fructose fraction from total glucose assayed in the "Clarase" digest.

Appendix 2

Laboratory gas-exchange measurement

An open system gas analysis apparatus was used, which utilised an infrared CO_2 analyzer (Beckman Instruments, model 865, Fullerton, California, U.S.A.), operated in both differential and absolute modes, and a dew point hygrometer (Cambridge Systems, model 880, Waltham, Massachusetts, U.S.A.). One attached intact leaf or phyllode was inserted in a well ventilated aluminium leaf chamber (boundary layer conductance to diffusion of water vapour was 2.2 mol m^{-2} s^{-1}). Illumination was provided by a 2.5 kW water-cooled, high pressure, xenon-arc lamp (Osram, model XBF 2500), the UV and IR components being removed with a Schott KG 2B filter. Quantum flux density (400-700 nm) was measured with a quantum sensor (Lambda Instruments, model LI-190 SR, Lincoln, Nebraska, U.S.A.). Leaf temperature, which was controlled by circulating water through a jacket, was measured with two copper-constantan thermocouples (0.1 mm diameter) in contact with the lower surface.

Air with a partial pressure of 320 mbars was obtained by injection of 5% CO_2 in air into CO_2-free air through a stainless steel capillary tubing. A self-venting pressure regulator (Clippard Minimatic, model MAR-IP, Cincinnati, Ohio, U.S.A.) and a pressure gauge were used to control the injection rate. The gas was passed through two columns of soda lime (Carbosorb, self-indicating, BDH Chemicals Ltd., Poole, England) and then humidified in a gas washing bottle with a scintered disc. The dew point of the gas was maintained by passing it through a glass condenser, the temperature of the latter being controlled by circulating the water from a temperature controlled water bath. Air flow through the leaf chamber was monitored with a mass flowmeter (Hastings, model AFSC-10K, Hampton, Virginia, U.S.A.). Flowmeters with needle valves were used to distribute gas flow through the system. Copper tubing was used in the circuit.

The outputs of all sensors were registered on a digital voltmeter and the outputs from the CO_2 analyzer and dew point hygrometer were continuously recorded. The outputs from the sensors allowed calculation of the rate of net CO_2 assimilation, stomatal conductance, transpiration of water and intercellular CO_2 partial pressure. All these parameters were calculated according to the equations given by von Caemmerer & Farquhar (1981).