Regeneration biology and silviculture of Tasmanian Soft Tree Fern *Dicksonia antarctica*

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SUMMARY

In recent years, commercial horticulture has provided an incentive to harvest mature *Dicksonia* stems from private and crown forests in Tasmania in order to supply Soft Tree Ferns at low prices domestically in Australia and to develop a very small market at high specially prices for export to Europe. Extraction and marketing of *Dicksonia antarctica* for export raised new issues of conservation and management of the native fern flora in Australia. At the same time, such an opportunity provided new avenues for research on the application of propagated growing stock and commercial silviculture of the tree fern within managed understoreys of fast-growing *Eucalyptus* plantations.

Project Objectives

(i) Preliminary investigation of regeneration biology and microclimate requirements for growth of Soft Tree Fern in native moist forest and in clearfelled plantation sites, notably to establish silvicultural requirements of the tree fern as a commercial understorey crop in *Eucalyptus* plantations, presently being widely established by large scale private forest companies in northern Tasmania.

(ii) Development of suitable techniques for nursery propagation, micropropagation, species provenance and site tolerance trials, suitable to complement and progressively to replace existing salvage of mature *Dicksonia* from field harvest, prior to reduction of the private forest clearance programme for plantation establishment.

(iii) Initial silvicultural trials of *Dicksonia* as an undercrop, specifically to place nursery stock of spore-propagated *Dicksonia* in young *Eucalyptus nitens* plantations of northern Tas.

Achievements

The project was proposed as a three year investigation with the above objectives. The Flora Foundation, RIRDC and Ausfern Pty Ltd. have supported this project financially and in kind for the first two years (1995 and 1996) with results as reported herein. The work continued as a limited holding operation during 1997 without funding. Continuation of comparative studies in Australian tree fern species, including *Dicksonia antarctica*, has now been approved by way of a commencement research grant with Southern Cross University, Lismore NSW, with an offer of $5000 which will allow silvicultural trials of this and similar species to proceed during 1998 and beyond.

Flora Foundation support for the investigation to date has also resulted in interest being expressed by forest ecologists in State Forestry Commissions. Research scientists consider the tree ferns may have application as possible indicator species in developing suitable criteria for maintaining and monitoring ecologically sustainable forest management practices (ESFM). The following report is based on progress reports, publications and commercial information produced by the authors during the course of this investigation. The report accounts for two years of investigation, as supported by the Flora Foundation and RIRDC. The following achievements are listed as milestones against the original objectives shown above.

Objective 1. Regeneration biology and microclimate requirements

(a) Completion of ecophysiological studies of *Dicksonia antarctica* (particularly in relation to photosynthesis and frond water relations);

(b) **Analysis and preparation of these results** for further publication and communication in scientific journals, international research groups and the popular horticultural press;

Objective 2. Propagation techniques

(a) **Training of a graduate student in developing techniques for micropropagation** of *Dicksonia* from field-collected spores and experimental callus culture;

Objective 3. Initial silvicultural trials of *Dicksonia* as an undercrop

(a) Establishing a working relationship with local nursery and plantation industries, purchasing, managing fern stock for outplanting; and

(b) Designing trials for **silvicultural underplanting of the tree fern beneath a young *Eucalyptus nitens* canopy** in a moist plantation site of northeast Tasmania (for underplanting mid-1998).

With due credit to the Flora Foundation, the results of this work have also been communicated among our research peers in Europe (Univ. of Edinburgh and British Pteridologists Society) and in the popular horticultural press in Australia (Australian Horticulture, Nov. 1996 and The Examiner newspaper, Launceston, April 1996). As well as hosting a fern visit by European tree fern specialist A. Wardlaw (Univ. of Glasgow) and the renowned plant physiologist RGS Bidwell in April 1996, the researchers have been invited to return to the British Pteridologists Society, London in the year 2000 to present the results of continuing silvicultural investigations of the tree fern species in proposed underplanting trials beneath fast-growing eucalypt plantations.

The Flora Foundation / RIRDC support of these investigations during 1995 and 1996 has been instrumental in developing international interest in a continuing tree fern research programme for future years (proposed and now accepted by way of Internal Research Grant, Southern Cross University for 1998). Even though financially limited in scale, the work has allowed the investigators to bring international attention to the prospect of cultivating and managing propagated tree fern populations silviculturally for an expanding world horticultural interest in Australian native ferns. The concept of actually raising and managing tree fern stocks for horticulture beneath rapidly expanding eucalypt plantations or disturbed farm forests, rather than simply exploiting or salvaging native populations for domestic or export sales, is somewhat new to Australian tree fern management (or our lack thereof). The Flora Foundation support for this research has enabled the investigators to focus international attention on tree fern conservation management with a degree of scientific authority hitherto lacking in the domestic horticultural trade among such species.

As outlined in the Project Proposal (16.5.94), our investigation of regeneration biology and microclimate requirements of the species is ultimately directed towards improved conservation of the Soft Tree Fern in eastern Australia, including assessment of opportunities for its silvicultural management in disturbed native forests and eucalypt plantations. Hence during 1995 and 1996, our *Dicksonia* studies have developed along two lines of investigation, both of which have involved a training component among graduates of Applied Biology at University of Tasmania:

(a) The ecophysiology of the species regenerating in eucalypt plantation forest understoreys (following from a successful invitation made to a B.App.Sci. (Hons.) student in 1994), and

(b) The development and training of techniques for micropropagation of the tree fern in controlled sterile conditions (undertaken by another student as part of a Grad. Dip. in Agricultural Science (Horticulture)).

The two lines of investigation were linked by the common objective of future propagation of the species for commercial horticulture, taking advantage of shaded understorey environments in forest plantations, in moist uplands of northeast Tasmania. Accordingly, the principal investigators have now established a secure partnership with a large prominent forest nursery in northern Tasmania (Mr J. Nicholson of Woodlea Forest Nursery via Scottsdale, Tas.) who is now providing in-kind assistance in the form of shadehouse maintenance of planting stock and well managed field sites for continuing stage 3 of the project (above), i.e. underplanting of *Dicksonia antarctica,* beneath young eucalypt plantations, during 1998.

In moist forest sites of northern Tasmania. present rate of *Eucalyptus* plantation establishment by large private corporations varies from 3500 - 4500 ha an^{-1}, depending on seasonal and operational conditions. This rate of conversion is set to treble as national goals of the proposed 2020 Vision programme are delivered in Tasmania. Additionally, tree growers on smaller family-owned farm properties are becoming increasingly well organised towards sustainable harvest and export of forest products from their collective forest estate. Tree Growers Cooperatives and the T17GA Farmwood Association in northern Tasmania are committed to optimal and sustainable long-term use of forest products from their farms, as a means to diversify and balance their agricultural operations, both financially and ecologically. The scale of farm forest development is ideally suited to improving productivity through small scale plantations and enrichment of disturbed native forest woodlots. Accordingly, there is particular interest in the next stage of the project, namely the design and development of experimental dual crop silvicultural systems for *Dicksonia* beneath young eucalypt plantations, planned to continue with the support of Southern Cross University research funding during 1998.

Results to date suggest that light, moisture and nutrient requirements of *Dicksonia antarctica* can be provided adequately in plantation forest understoreys or beneath disturbed native forests, without compromising either the productivity of the plantation or the ecological succession of native forest gaps. As follows in this report, plant-microclimate analysis and canopy/understorey comparisons indicate that declining vapour pressure deficit exerts a stringent control on foliar gas exchange in *Dicksonia*, such that the species has very conservative water use during seasonal and diurnal dry spells. The analysis suggests that atmospheric water relations and intolerance of direct sunlight determine the adult growth behaviour of *Dicksonia* in plantation forest understories, as opposed to microsite condition and availability of free water which limits field germination and initial establishment from spores. This has important implications for dual crop silviculture as the conservative tree fern species appears ideally suited to understorey conditions, by and large avoiding adverse competitive effects on the fast growing canopy eucalypt.

Techniques for sporophyte propagation of *Dicksonia* from prolific yields of wild spores are well established (M.Garrett, pers. comm.; Goudey & Hill, 1986). *In vitro* propagation of sporophyte tissues also offers promise in relation to cloning and multiplication of isolated or threatened genetic material. In the present study, protocols and media requirements for the *in vitro* propagation of sporelings of this important native fern species were derived experimentally, with replicated factorial trials for sterilisation, germination and culture on agar. Development of a suitable methodology included techniques for measurement of prothallus size (maximal diameter) *in situ* on sealed agar plates, to avoid the risk of contamination. Growth responses of gametophyte plants to auxin and cytokinin additions to the media were interactive with sugar concentration. Development work also included culture trials using explants of sporophyte tissue taken from fern fronds, both from young crozier material and using pieces of adult frond. As anticipated, sterilisation proved a critical problem with adult explant material. Cultures using young frond material remained healthy for several months but did not produce differentiated frond or root tissues from cultured explant material.

Results of the project have sustained. our cautious prospects for sustainable silvicultural production of advanced adult tree ferns in moist plantation understoreys. Difficulties associated with the absence of funding during 1997 and the interstate transfer of both authors during the same year, have now been overcome. Silvicultural establishment trials will continue with S.C. University support for outplanting present stocks of nursery propagated sporelings in the plantation understorey, during 1998. This field application of results will ultimately put to the test our explanation of plant-environment relations derived experimentally through ecophysiological investigation of *Dicksonia antarctica*, as outlined in the following report.

Publications and reports generated as a result of this study are listed as follows:

1996. Unwin, G.L. and M.A.Hunt. Conservation and management of soft tree fern *Dicksonia antarctica* in relation to commercial forestry & horticulture. In: J.M. Camus, M. Gibby and R.J. Johns (Eds.), *Pteridology in Perspective*. pp. 125-137, Royal Botanic Gardens, Kew, London.

1996. Unwin, G.L. and Hunt, M.A. Towards a functional definition of understorey: Canopy and understorey processes in relation to farm forestry. Keynote address, Understorey in Farm Forests, Understorey Network and Univ. of Tasmania, Nov. 1996, Launceston, Tas.

1995. Unwin, G.L. and Hunt, M.A. Regeneration biology and silviculture of Tasmanian Soft Tree Fern *Dicksonia antarctica*. Ausfern P/L., Tree Fern Associaton of Australia and Australian Flora Foundation. Progress Report, 30pp.

1994. M.A. Hunt, N.J. Davidson & G.L.Unwin. Carbon and water relations of *Dicksonia antarctica*: *A* **preliminary investigation.** Aust. Soc. Pl. Phys., Qld. September 1994.

(1998). Hunt, M.A., Davidson, N.J. and G.L. Unwin. Ecophysiology of Soft Tree Fern *Dicksonia antarctica.* Aust. J. Botany. *12pp.* (Submitted).

1. INTRODUCTION

This Report examines the ecology and physiology of *Dicksonia antarctica* and provides an overview of results for work commenced during 1995 and 1996. As outlined in the Project Proposal (16.5.94), the investigation of regeneration biology of the species is ultimately directed towards improved conservation of the Soft Tree Fern in Tasmania, including assessment of opportunities for its silvicultural management in native forests and eucalypt plantations.

During 1995 and 1996, the *Dicksonia* studies developed along two lines of investigation - the ecophysiology of the species regenerating in eucalypt plantation forest understoreys and the development of techniques for micropropagation of the tree fern in controlled sterile conditions. The two investigations were linked by the common objective of future propagation of the species for commercial horticulture, taking advantage of shaded understorey environments in forest plantations, in moist uplands of northwest Tasmania. As a result of our work, we emphasize the need to regulate and manage effectively the impact of salvage harvesting of mature Soft Tree Fern, in order to protect future forest values and to sustain the benefits of the species for horticulture.

With ecologically sound resource management and regulation, the commercial harvest and propagation of *Dicksonia antarctica* for local, domestic and export markets have the potential to provide an important sustainable industry for south~ eastern Australia. This report will focus on conservation and management implications for Tasmania where the native distribution of this fern species is widespread. However, the observations to be made are generally applicable to conservation management of this tree fern resource elsewhere in south-eastern Australia, wherever commercial sale or harvest of the species is to be entertained.

We first consider the regeneration biology and ecophysiology of this tree fern in native forest understories and then relate growth requirements of the species to observed microenvironments in commercial *Eucalyptus* plantations. Based on analysis of canopy-understorey interactions, this investigation points cautiously but optimistically towards dual-crop silviculture of the Soft Tree Fern beneath commercial stands of *Eucalyptus.* On smaller scales, e.g. private farm forests, *Dicksonia antarctica* may be introduced beneath otherwise disturbed canopies of desirable cabinetwood species (e.g. *Acacia melanoxylon).*

In Tasmania, a maritime, mild to cool temperate climate prevails, very moist in the western and southern half of the state, seasonally warm and dry in summer, especially in the north and east. D. antarctica or Soft Tree Fern (otherwise known locally as Manfern) is the most common of five tree fern species found among a variety of moist forest types across elevations from sea level upwards to 1000m. Habitat range varies from restricted riparian communities and microsites within generally 'dry sclerophyll' Eucalyptus woodlands, through well-developed tree fern understories of tall moist eucalypt forests and mixed forests which are themselves transitional to Callidendrous rainforest (Kirkpatrick, 1991).

Although tree ferns on mainland Australia are protected by state flora and fauna legislation, Tasmanian tree ferns are unprotected except in designated reserves, conservation areas and national parks. This resource presents definite opportunities for sustainable horticultural use of such an attractive, versatile and abundant tree fern species. However, there are increasing national and international responsibilities to manage and regulate such use with appropriate and effective conservation of natural populations and habitats, as genetic, if not morphological diversity, is to date largely unknown.

The statewide population estimate of the Soft Tree Fern in Tasmania (Table 1) is acknowledged as approximate at best, based on only twenty transect samples of native tree ferns across eight moist vegetation types where the species is most common (Neyland, 1986). Extrapolation was achieved by computerised overlay of the Kirkpatrick & Dickinson (1984) vegetation map and land tenure maps at 1:500,000 scale (Forestry Commission, 1989). The estimate confirms that the Soft Tree Fern resource is large, on a statewide basis (N= 119.3 x 10^6 stems). However, the precision of this estimate is unknown and no attempt has been made to assess individual populations or the impact which present and past cutting practices and removals have had on local population densities.

At present, the tree fern industry is based on les s-than- adequate control of domestic harvest for low-priced and low-return local and mainland markets. Although domestic trade is focussed on two states, from Tasmania to Victoria, the local industry is fragmented and uncoordinated. Pilfering, price cutting and unpaid royalties are common among less scrupulous domestic operators, to the detriment of crown and private landholders and to the frustration of those longer term harvesters and plant dealers who care for the sustainable future of native fern populations and of their industry. Currently, only around 70,000 stems of the estimated 160,000 sent to the mainland domestic market annually are accounted for by royalty (Ausfern P/L, based on 1993-94 estimates).

Table 1. Summary of population estimate of *Dicksonia antarctica* in Tasmania, by broad forest formation and tenure, based on an extrapolation from eight moist forest types where the species is a common component (Neyland, 1986; Forestry Commission, 1989). Numbers are of stems x 10^6.

	EUCALYPT FOREST TYPES	RAINFOREST TYPES	TOTAL
Unreserved State Forest and Crown Timber	63.6	6.5	70.1
Crown Reserve Conservation Area and National Park	16.4	7.0	23.4
Private Land	23.9	0.65	24.6
Other	1.1	0.06	1.2
TOTAL	105.0	14.30	119.3

Although not immediately threatened, the Soft Tree Fern is a CITES-listed species in relation to export trade (Convention for International Trade in Endangered Species). Utilization of native tree ferns for the purpose of developing small but potentially high-priced and well-targeted export markets has, by Commonwealth control, been very much restricted to genuine salvage harvest of the species. Salvage of mature stems for export therefore has been constrained to situations where other land uses (such as forest clearance for eucalypt plantation establishment, roads, power transmission lines etc.) would result in the immediate destruction of both these and other ferns, accompanied by the possible loss of an unknown portion of their genetic variation.

Physiological studies reported herein suggest that dual-crop plantation systems or enrichment planting of disturbed forest understoreys may provide the future means of integrating both domestic and export requirements for sustainable harvest of *Dicksonia antarctica.* This report examines such opportunities, starting with essential regard to the biology of the species.

2. FLORAL HISTORY AND ECOLOGY OF *D. ANTARCTICA*

South-eastern Australia, in particular the island of Tasmania, is well blessed with many fine examples of fossil tree ferns confirmed of Jurassic age, overlain by basalt and dated at about 140 - 160 million years ago (Ma) (Tidwell *et al.* 1989; White, 1993). These volcanic eruptions and the fossil flora laid down foreshadowed the emerging breakup of the giant southern supercontinent Gondwana. Australia, however, was not to separate from Antarctica for another 100 million years (55Ma). Since the Oligocene or Miocene (35-25 Ma), Tasmania has periodically remained either a peninsula of mainland Australia, or an island, rather like the last appended carriage on this slow, northward-moving train, which is the Australian continental plate (Hill, 1990). On this grand continental journey northwards through 13º latitude, the resident floral baggage included cyathean tree fern genera, the antecedents of modern day *Dicksonia* and *Cyathea*, as a prominent component of the Antarctic flora which remains intact in moist parts of Tasmania to this day.

At Lune R. in the far southern corner of Tasmania, well preserved fossil ferns commonly include specimens of the primitive ‘Palaeosmunda' tree ferns, e.g. *Osmundacaulis jonesii* (Tidwell, 1987) and 0. *nerii* (Tidwell & Jones, 1987) whose affinity relates to present day *Todea barbara* of eastern Australia, (incl. Tas.), New Zealand and South. Africa and T. *papuana* of New Guinea. Elsewhere, in both southern and northern hemispheres, osmundalean ferns are traceable even further in the fossil record to the much older Permian period, at about 260 Ma (White, 1991).

Also found in the Jurassic tree fern flora of Lune R. are the cyathean examples described as *Oguracaulis banksii* (Tidwell *et al.*, 1989) and *Cibotium tasmanense* (Gould, 1972). It is therefore about this time in the Australian fossil flora (140- 160 Ma) that the story of the present day Australian Dicksoniaceae and Cyatheaceae begins. (Extant species of *Dicksonia* and *Cyathea* in Australia number two and 11 respectively (Jones & Clemesha, 1989). There are three species of *Dicksonia* in New Zealand. In some classifications, the genus is treated as a more primitive subfamily of Cyatheaceae (Duncan & Isaac, 1986).

Dicksonia antarctica is one of Australia's most widespread tree ferns found in all eastern states from southeast Qld., through eastern NSW and Vic. to Tasmania (Jones & Clemesha, 1989). The species prefers moist forest understoreys and shaded gullies in high rainfall areas, is frequently found in partially shaded rainforest gaps resulting from tree falls or small patches of disturbance, though it is not common in very densely shaded understoreys of mature rainforest. The Soft Tree Fern is particularly prominent along moist forest edges and vigorously colonizes shaded road embankments in moist highland forests of the southeast. (Although *D. antarctica* was formerly to be found in restricted moist forests of South Australia, the species is now believed to be locally extinct, through forest clearance and cutting which has occurred following European settlement and agriculture.) Ironically, S. Australian provenances of *D. antarctica* are today found alive and regenerating well in mild temperate gardens of Cornwall and elsewhere in Europe as a result of such cutting and early export, having contributed prominently to the so-called European fern craze of the mid-19th century (King, 1985; Nelson, 1992).

The growth habit and biology of Soft Tree Fern appear to have changed little from its early origins in the mesic, temperate Gondwanan flora to which it belongs. Today, the species is widespread in Tasmania, especially on fertile, moist forest sites receiving mean annual rainfall (m.a.r.) of 1000 mm or more (Neyland, 1986). The species is a common, attractive component of moist forest understoreys beneath tall canopies of *Eucalyptus* spp. or *Acacia melanoxylon* (Tasmanian blackwood forests) and is also characteristic of young or disturbed rainforests, mixed (rainforest/eucalypt) forests and transitional or ecotonal rainforest understoreys.

In seasonally dry and fire-prone sclerophyll forests and grassy woodlands of 600-1000 mm m.a.r., (the essentially autochthonous Australian flora, including much of the north-eastern half of Tasmania), distribution of *Dicksonia* is limited to shaded gullies and streamside gallery forests. In such microsites, alluvial soils are often fertile and atmospheric and surface moisture availability, if not topographic protection from fire, is likely to be the critical determinant to riparian distribution.

The tolerance of adult *Dicksonia antarctica* to fire injury is a notable, though common fern attribute, which at first glance appears to sit curiously alongside more fire-sensitive coniferous and angiosperm elements of the Australian-Antarctic flora. Individual mature stems of *Dicksonia* are adapted to vigorous early recovery along infrequently or lightly burned rainforest edges or moist gullies, and in mixed forest understoreys irregularly visited by fire (Hickey, 1994). However, in studies of intensive canopy disturbance such as logging followed by slash burning to promote seed regeneration of *Eucalyptus*, tolerance of the tree fern to intense fire is reduced and is conditional on the maturity and size (height and girth) of the upright stem (Peacock, 1994). The tree fern caudex appeared to require sufficient size and bulk (approx. lm height or more) to confer upon the deeply embedded frond meristem or crozier a sufficient degree of thermal insulation. A blackened and much reduced survivor may, with favourable post-fire microclimate, produce rapid renewal of fronds following moderate to high intensity fire, though net losses may be high (50-90 %). As well as smaller ferns (<lm), tall stems of the tree fern. (> 2.75 m) and those adjacent to fallen, burning timbers were also at increased risk.

The regeneration biology of *Dicksonia*, as with other ferns, is dependent on viable spore delivery to a suitable substrate with appropriate conditions of moisture, nutrients and microclimate. The sequence of events in the development and life cycle of *Dicksonia antarctica* is well documented (e.g. Page, 1979).

Regeneration is a four-stage process (Neyland, 1986), consisting of.

(i) spore germination and prothallus production (the gametophyte phase, of several weeks duration);

(ii) fertilisation and sporophyte emergence from the prothallus, lasting up to two years depending on conditions; leading to

(iii) the rosette or young sporophyte stage in which true fronds, root system and finally a central stem are formed; and

(iv) growth of the mature adult, complete with upright woody trunk (the caudex), large spreading and ultimately fertile fronds.

Availability of moisture is critical to establishment of the prothallus and to the successful fertilisation of the female archegonia by motile sperm cells. Thereafter, continuing atmospheric and substrate moisture availability, the immediate light environment and allelopathic effects are observed to be instrumental to the regeneration of healthy, vigorous sporophyte populations in forest understoreys (Neyland, 1986).

Of particular importance in the present context however, is the possible distinction in environmental tolerance and microclimate requirements suitable for:

(a) gametophyte / sporophyte establishment and regeneration, (stages (i)-(iii) above), and

(b) growth of the adult sporophyte, (stage (iv)),

when central stems, unfurling croziers and root systems have already become established in the forest understorey, leading in time to mature tree ferns.

On this distinction rests the essential difference between (largely uncontrolled) requirements for natural regeneration in the moist forest understorey and opportunities offered by nursery-based propagation. Propagation, understorey planting and silvicultural establishment beneath disturbed forests and plantations may provide suitable future direction for the conservation and management of *Dicksonia antarctica.* Niche requirements for natural regeneration and early establishment in the forest understorey are likely to be more exacting, especially in terms of necessity for free moisture and high levels of atmospheric humidity, than are conditions required for subsequent growth of the mature adult. Neyland concludes *'it is conditions for germination of the spore and prothallial development and then development of the young sporophyte that are critical for the survival* [and hence establishment] *of tree ferns on a site'.*

The existing natural distribution of *Dicksonia antarctica* in eastern Australia, especially in relation to regional gradients of declining rainfall, reflects this critical early requirement for available moisture. At smaller scales, within understoreys of established *Eucalyptus* plantations, microsites for natural recruitment of new sporophytes are often limited to small, shaded reservoirs of entrapped moisture in cut stumps, root hollows, moss beds or elsewhere on fallen phorophytes, where free moisture remains and high humidity prevails. A similar microsite distribution for establishment of sporophytes emerged in studies of recovery and regeneration of *Dicksonia* following forest logging and burning (Peacock, 1994).

Silviculture of propagated *Dicksonia* in plantation understories will largely circumvent the stringent early microsite requirements of the regeneration phase. By comparison with reproductive requirements, continuing development and growth of adult *Dicksonia*, once established, will depend on optimal physiology of essential photosynthetic, storage, water and nutrient functions. These essential components for growth have largely been established in vigorous young *Dicksonia* stems beyond the regenerative and establishment phase of their development. For this reason it is necessary to look to the ecophysiological requirements for stem growth and foliage function, as opposed to regeneration biology, in considering longterm horticultural opportunities for propagation-base d conservation management of this species.

3. SPOROPHYTE GROWTH AND NICHE REQUIREMENTS IN FOREST UNDERSTOREYS

The distribution and autecology of *Dicksonia antarctica* illustrate this species' preference for intermediate, transient light conditions, i.e. those conditions characteristic of tall forest understoreys, small canopy gaps in rainforests, shaded gullies and forest edges. As reported above, there is substantial evidence that the regeneration and establishment phase is limited primarily by microsite moisture conditions, in particular the requirement for prevailing high moisture levels in the immediate environment of the prothallus and young sporophyte.

To identify physiological niche requirements for growth of the adult sporophyte, it is therefore pertinent to examine the species' photosynthetic response to understorey light and moisture conditions, including foliage stomatal response to soil moisture and atmospheric moisture availability.

Forest understoreys have been shown elsewhere to be light-limiting environments, to the extent that light distribution, both spatially and temporally, most strongly influences water use, photoassimilation and ultimately the growth and regeneration of such flora. Poor water use efficiency (the amount of carbon gained per unit of water consumed by evapotranspiration) is a typical price to be paid by some understorey plants for being primarily light adapted (Black & Kelliher, 1989). In generally low light environments, this behaviour provides for short term productivity boost when light is available, even though immediate transpiration losses may be substantial due to high evaporative demand and weak or ineffectual stomatal control. However, the nature of tree fern morphology and growth habit dictates closer scrutiny of general trends, in this case in terms of the plant-environment interactions displayed by *Dicksonia* in the forest understorey.

Nobel *et al.* (1984) examined a range of light responses in 14 fern species, including *D. antarctica.* Sporophytes of unspecified age were grown in a glasshouse under conditions of moderate light, temperature and humidity. (Average daily PPFD 11 mol $m^{-2}day^{-1}$, max PPFD 1000 uE $m^{-2}s^{-1}$; Temp. range 20-27ºC R.H. 55-85%) Among the species investigated, the degree of stomatal response to atmospheric vapour pressure deficit (VPD) increased according to the magnitude of stomatal conductance at low VPD, i.e. the higher the fern's foliage conductance under moist, idealised conditions, the more pronounced was the negative stomatal response to less favourable conditions of increased VPD. Within this range,*Dicksonia* demonstrated intermediate foliage conductance and a moderate stomatal sensitivity to VPD (reduced humidity and/or increased temperature).

In a more recent, Tasmanian study *in situ* in a moist forest understorey (Hunt, *1993), D. antarctica* indicated a pronounced response to VPD (Fig. 1), commencing even at low VPD levels associated with high relative humidity. Maximum stomatal conductance was almost double the value evidenced by Noble *et al.* (1984) (0.44 vs. 0.24 cm s^{-1}*).* Maximum photoassimilation rate for *Dicksonia* was 10.8 µmol $C0_2$ $m^{-2}s^{-1}$ by Hunt, in field conditions and 8.3 µmol $C0_2$ $m^{-2}s^{-1}$ by Noble in the glasshouse study. Most relevant in the present context is that light saturation was evidenced at relatively low levels of irradiance in both studies, with 90% saturation occurring at 220 µE $m^{-2}s^{-1}$ (Fig. 2), an order of magnitude characteristic of shaded forest conditions beneath intermediate canopy cover. (Max. photosynthetic rates quoted are in fact quite high in both reports of *Dicksonia,* compared with other fern species investigated.)

Collectively, the physiological evidence confirms that the tree fern is capable of high rates of carbon fixation at light intensities approximating 10% of full sunlight. Such light conditions are appropriate to partly shaded canopy gaps and forest edges but exceed generally low light levels experienced beneath the dense closed canopy of undisturbed rainforest (c. 10-50 uE $m^{-2}s^{-1}$). Furthermore, availability of atmospheric moisture and the leaf-to-air water vapour gradient (vpd.) continue in the adult sporophyte to exert a primary influence on short term productivity and growth, as evidenced by the reported stomatal response to VPD.

Anecdotal and experimental observations indicate the capacity of mature *Dicksonia* to survive and indeed to flourish in the absence of soil or other substrate and without application of water to the roots or stem from below. Such observations have been confirmed on numerous occasions in both forest understoreys and in the nursery. It is widely observed in horticultural use that following removal from the forest floor, harvested stems of *D. antarctica* will produce a new crown of functional fronds, generally within twelve weeks, without any application of water. In the forest understorey, the funnel-like architecture of the frond rosette is ideally configured to concentrate both throughfall and litterfall towards the living apex of the growing fern. The tree fern is therefore exquisitely adapted to intercept rainfall, throughfall and decomposing litter in the forest understorey and to direct both water and dissolved nutrients towards hydration and nutrition of the large reservoir in the bulky upright stem. As field evidence suggests, the mature adult sporophyte is thus effectively decoupled from the soil.

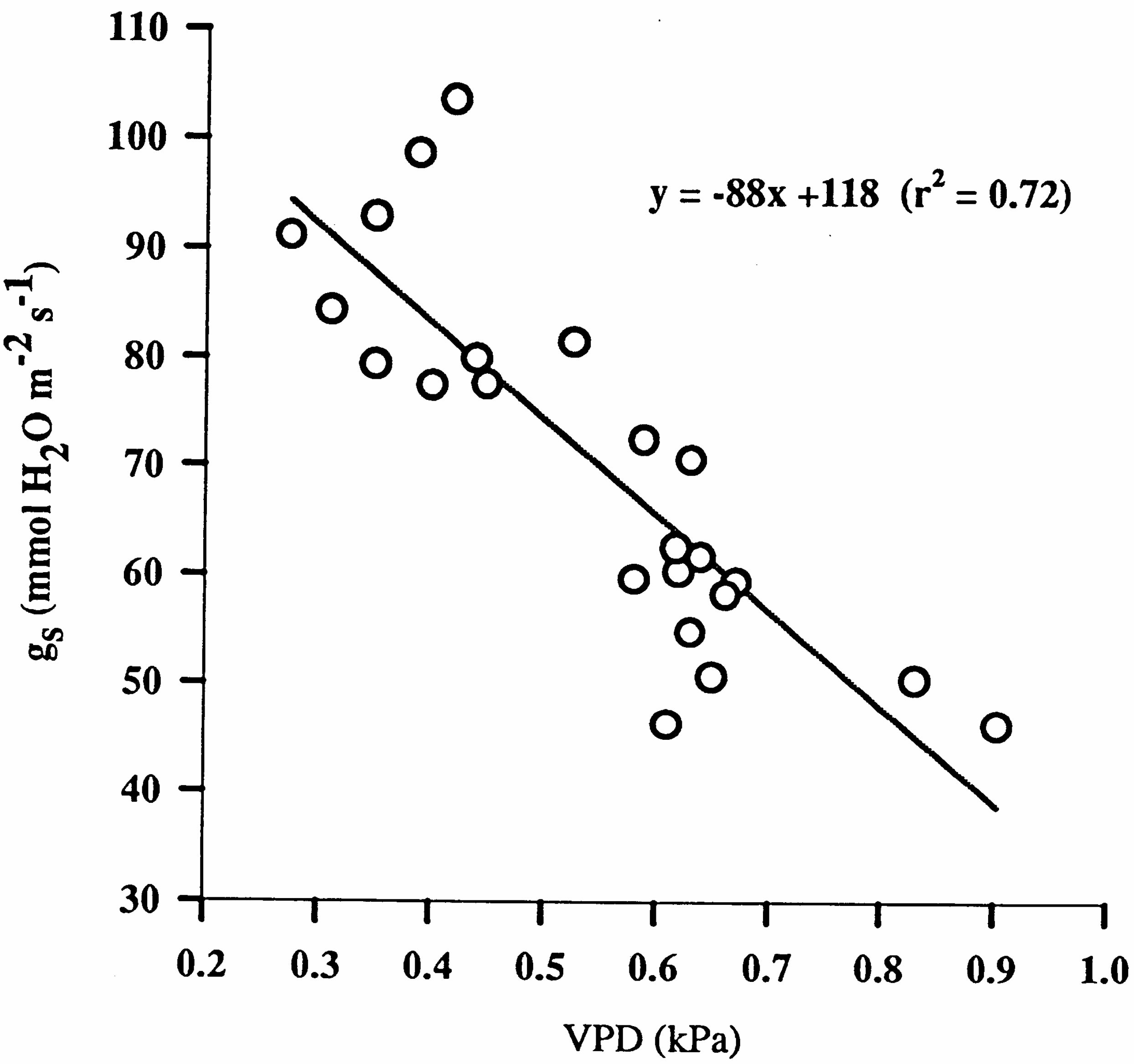

Fig.l. Relationship between stomatal conductance of understorey *D. antarctica* (g_s) and atmospheric vapour pressure deficit (VPD).

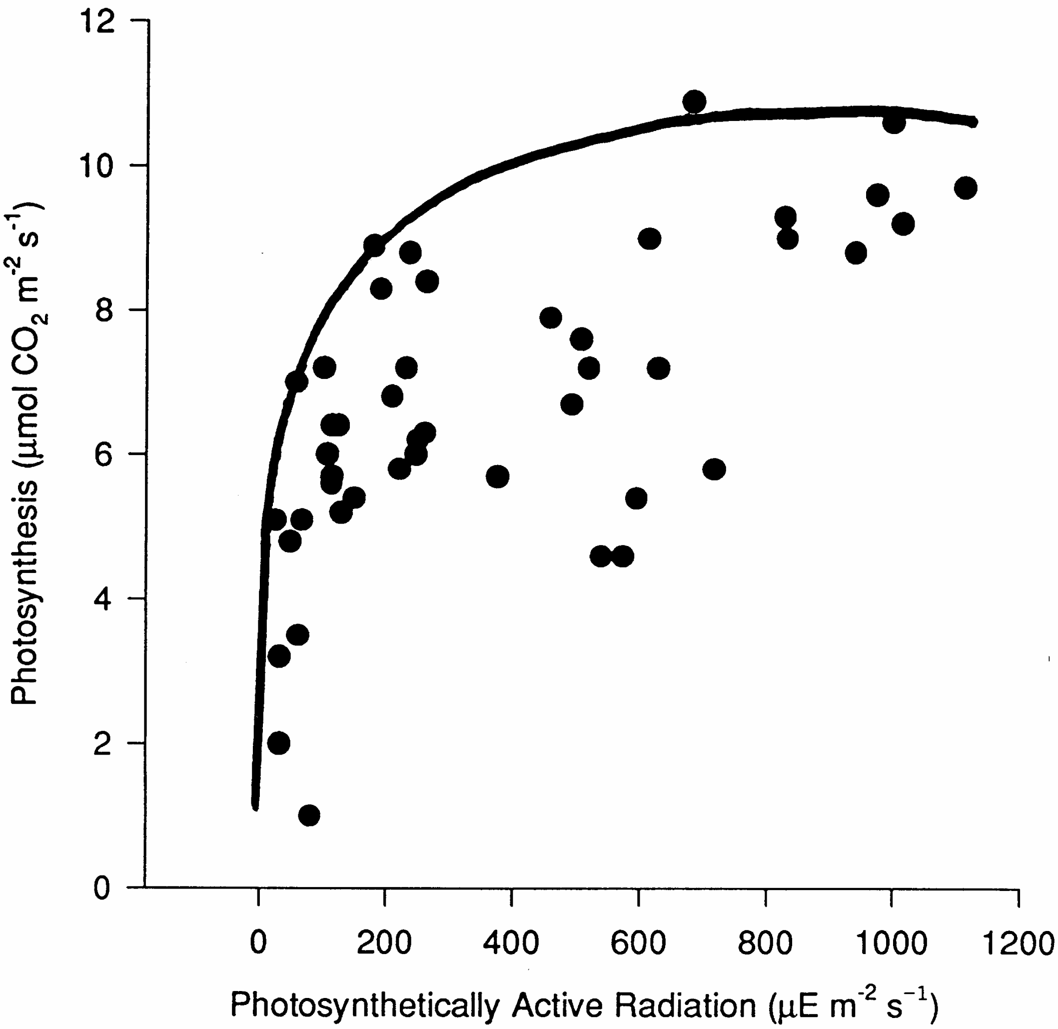

Fig. 2. Photo-assimilation response of understorey *D. antarctica* to photosynthetically active radiation (PAR). (Curve shows approximate boundary line of maximal values, after Hunt, 1993.)

An interesting aspect of the above physiological studies is that frond stomata respond to declining moisture availability (increased VPD), even when the stem is fully saturated with water (by soaking for several days). Such VPD response also occurs in the absence of any measurable change in frond water potential. The strong stomatal response to VPD therefore appears to be independent of both plant and soil water status. Walter and Stadelmann (1974) reported that pteridophytes can have a poor water conducting system and Nobel (1978) measured a steep gradient in water potential along the stipe of *Notholaena parryi* (-10MPa m^{-1}) which he attributed to a small conducting cross-section (relative to leaf area) in the xylem. It is also observed that tracheids are more prone to cavitation and embolism than are vessels of the same dimensions (Tyree & Dixon, 1986). Fronds of mature *Dicksonia* regularly exceed 3m length. Were high rates of evapotranspiration to occur for any length of time in the absence of stomatal regulation, promoting water potential gradients of the magnitude reported by Nobel (1978), the frond may be at risk of catastrophic embolism in the stipe. In such circumstance, a strong stomatal response to declining humidity and increasing VPD would provide an effective safeguard.

An alternative explanation for the extremely conservative water use strategy of *D. antarctica* is that as an understorey plant of considerable size and foliage proportion, it will frequently need to conserve water during seasonally dry conditions. Even in moist forests, the late summer period in south-eastern Australia can produce just such a pattern of temporary water deficit over much of the natural distribution of *Dicksonia.* The immediate impact of seasonally dry conditions is exacerbated in the forest understorey by strong water demand of the immediate overstorey, especially in the form of fast growing, large forest trees such as *Eucalyptus* spp. It is therefore necessary to consider the influence of the tree canopy on understorey microclimate and water relations if we are intent on investigating the productivity of tree fern silviculture in eucalypt plantations or disturbed native forests.

4. CANOPY - UNDERSTOREY INTERACTIONS IN MOIST FORESTS AND *EUCALYPTUS* PLANTATIONS

Strong stomatal response to relative humidity, the observed photosynthetic response to low light and effective decoupling of mature *Dicksonia* from the soil water environment - all have important implications for tree fern productivity in native forest and plantation understoreys. Each of these attributes relates directly to the growth and phenology of mature *Dicksonia* in the understorey microclimate which itself is largely determined by interactions with the forest canopy.

The authors have studied plant water use and micrometerology within a 17 year old *Eucalyptus nitens* (Deane and Maiden) Maiden plantation forest whose understorey includes a significant component of mature *Dicksonia antarctica* (stem heights 1-2 m, crown widths 2-4 m). These ferns are those which have recovered from the original native forest understorey, following plantation establishment in the moist uplands of north-western Tasmania. The eucalypt plantation is typical of the higher rainfall sites with fertile soils, currently being converted from mixed native forest to privately owned tree farms in the north of the State (establishment rate 3500-4500 ha yr^{-1}).

In this study of canopy / understorey water relations and micrometerology, foliar gas exchange was limited diurnally by reduced insolation and low temperature during autumn and winter and by a combination of high insolation and VPD during spring and summer (Hunt, 1993). Repeated predawn estimates of leaf water potential indicate that soil moisture availability was sufficient to ensure rehydration of the eucalypt canopy overnight, precluding any accumulated seasonal water deficit at such sites. Even so, steep gradients in sunlight, relative humidity and VPD were recorded regularly between the forest canopy and the understorey, characteristic of limited energy flux and turbulent transfer through such vertical profiles.

On days of high insolation, irradiance of the understorey is much less than in the canopy (only 5-10 %), implying a sharp reduction in the energy available to raise diurnal temperatures of the forest interior or to reduce relative humidity in the understorey. Soil is typically at field capacity during winter and remains moist through most of the year. Energy incident on the forest floor is therefore dissipated as latent rather than sensible heat, in contrast to the canopy where, once leaves are dry, dissipation of latent heat occurs only via transpiration. Under such conditions, relative humidity will remain much higher in the understorey than in the overstorey. It is therefore probably a function of aerodynamic mixing, the amount and/or frequency of bulk air penetration (turbulence) into the understorey that determines vertical gradients in relative humidity and VPD, within the forest profile.

Humidity gradients exceeding 30% were measured repeatedly and relative humidity in the understorey frequently ranged between 80% and saturation for weeks at a time. Corresponding microclimate regimes have been measured and described for native forest boundaries and canopy gaps in closed forests (Unwin, 1983).

Given the interactions of moisture availability and sunlight as recorded in such canopy profiles, the plantation understorey appears to provide a near-optimal environment for advanced growth of sporophytes, particularly in view of the known autecology of *Dicksonia antarctica.* Sunlight in the shaded understorey is generally below saturation levels for this species for much of the time (Fig. 2). However, sufficient light is available for intermediate rates of photosynthesis to continue, particularly as the prevailing high humidities of the understorey will most often preclude the demonstrated stomatal sensitivity to VPD. Furthermore, the abrupt rise in the photosynthetic / light response (Fig. 2) ensures that periods of maximum short-term productivity are facilitated by frequent sunflecks afforded by the overstorey.

In brief, the microclimate condition offered by the plantation overstorey or native forest canopy ensures that growth of *D. antarctica* in the understorey is rarely limited during the day, either by light or by evaporative demand. Overstorey protection is such that in moist forests, more extreme VPD conditions external to the forest (low relative humidity, seasonally high temperature), are rarely if ever, sufficient to induce high VPD in the understorey with the associated response of stomatal closure in the tree fern.

Seasonal conditions of low or infrequent rainfall may limit the opportunity for the tree fern to harvest sufficient water for adequate stem recharge. Although interception by *D. antarctica* in the understorey is yet to be quantified, eucalypt canopies have been shown to intercept up to 25% of individual rainfall events (Lima, 1984). In view of the proposed importance of aerial collection of water and dissolved nutrients by the frond rosette of the fern, it is possible that during seasonally dry conditions, interception by canopy trees such as plantation eucalypts may deny the understorey fern an adequate water supply, especially if soil moisture is also in competitive demand. However, with increasing bulk of the fibrous caudex of the tree fern with age, hydraulic capacitance of the stem increases and extended drought periods would be required to exert lasting detriment to fern productivity. Likewise, the strong stomatal response to atmospheric VPD will assist the fern to conserve stored water during such conditions. If the surface soil is seasonally dry and there is little rainfall to penetrate the overstorey, *D. antarctica* may continue stomatal function and gas exchange for brief but productive periods in the understorey each day. This conservative water use strategy could well serve to prevent the development of severe drought stress (and untimely death) in the fern during unusually dry summers.

There remains the inverse question of understorey effects on canopy productivity. In dense understoreys of *Dicksonia,* efficient concentration of throughfall water by the fern rosette may reduce soil recharge and hence limit soil water availability to the canopy. However, in the case of *Eucalyptus* plantations, the deep feeder root system of the eucalypt, coupled with high annual rainfall at sites of interest, suggests that such an influence may not be significant. Other understorey species in native forests and eucalypt plantations are likely to display more aggressive water use strategies than the ultra-conservative *Dicksonia.* It is reasonable to imagine that a large but conservative *D. antarctica* component in the understorey may process less water per unit area than a mixture of vigorous early successional broadleaf species which might otherwise colonise canopy gaps or plantation understoreys. It is possible that a substantial presence of *D. antarctica* in the understorey actually increases the proportion of available water resource to the canopy, compared to other understorey species, even though some throughfall interception by the tree fern will occur. Research effort could usefully be directed to quantify such interactions in detail.

5. RESOURCE USE, CONSERVATION and SILVICULTURE

Salvage vs silviculture: a lesson in sustainability

In October 1994, the Commonwealth placed a moratorium on all export of native *Dicksonia* stems, salvage harvested or otherwise, acting on the advice of its own CITES-designated authority, the Australian Nature Conservation Agency. ANCA invoked the moratorium pending implementation and Commonwealth approval of a state-wide resource management plan for regulating the harvest, conservation and effective protection of native *Dicksonia* populations on both crown and private lands in Tasmania.

In this context, possible opportunities for silvicultural production of mature *Dicksonia* offer an attractive medium and long-term strategy, leading from the present unregulated domestic harvest of native tree ferns towards a propagation based industry for both domestic and export horticulture. At face value, this strategy appears both commercially efficient and of good conservation practice. Genuine salvage harvest of native forest specimens is a wholly desirable and necessary short-term response to their imminent destruction. (The same argument applies to a number of other fern species so affected.) However, such immediate resource availability is limited by the merits and outcomes of other land use decisions, e.g. the incidence of forest clearance for plantation establishment. Whilst providing an immediate source of tree ferns which would be more than sufficient to meet demands of a properly regulated industry at present, salvage harvest is a sensible but transient option only. This short term supply should be seen as part of a longer term conservation strategy aimed at maintenance of existing genetic stocks and the carefully planned development of a propagated tree fern resource for future sustainable harvest.

To date, the harvest of Soft Tree Fern from both private and crown lands in Tasmania has been largely uncontrolled. The one management plan currently operating (Forestry Commission, 1989) applies to State Forests only, without the necessary resources being available to discourage widespread poaching of tree ferns from either crown or private lands. These are then dumped on the domestic market, some locally but the large majority is sold cheaply on the mainland, through Victoria.

Federal and State authorities (ANCA, Canberra & Parks and Wildlife Service, Tasmania) have both now recognised the urgent need to regulate and to manage effectively the use and protection of the existing large tree fern resource in Tasmania. The present Commonwealth moratorium on export of *D. antarctica* has prompted serious and active review of the existing use of this species and it is promising to note that a new State-wide management plan is currently being proposed in consultation with existing tree fern harvesters and nurseries.

The proposed management plan is based on licenced salvage harvest, tagging and accounting of fern stems from point of harvest to point of retail sale. Licence fees and purchase price of tags will constitute a levy on the controlled harvest of this resource, providing funds for resource monitoring and conservation research of the species. A programme for replanting of *Dicksonia* to complement remaining native populations is envisaged. Careful use and protection of streamside reserves according to the Tasmanian Forest Practices Code (Forestry Commission, 1993) is seen as a critical step towards conservation of existing genetic resources of *Dicksonia.* This is especially the case in areas where logging or clearfelling of native forest populations is continuing e.g. for establishment of extensive corporate tree farms for pulpwood production.

In moist forest sites of northern Tasmania, present rate of *Eucalyptus* plantation establishment by large private corporations varies from 3500 - 4500 ha yr-1, depending on seasonal and operational conditions. Additionally, tree growers on smaller family-owned farm properties are becoming increasingly well organised towards sustainable harvest and export of forest products from their collective forest estate. Tree Growers Cooperatives in northern Tasmania are committed to optimal and sustainable long-term use of forest products from their farms, as a means to diversify and balance their agricultural operations, both financially and ecologically. The scale of farm forest development is ideally suited to improving productivity through small scale plantations and enrichment of disturbed native forest woodlots. Accordingly, there is particular interest in design and development of dual crop silvicultural systems suggested in this paper for *Dicksonia.*

The conservation and management of this versatile and impressive fern species may best be considered in terms of the phased restructure and progression of the existing uncoordinated industry from salvage harvest towards propagation and sustainable silviculture. The currently proposed tree fern management plan for *Dicksonia antarctica* provides a unique and timely opportunity to secure a sustainable future for longterm horticultural use of this species. Concurrently, the present review offers a mechanism for implementing effective research and protection of extensive native populations of this and associated fern species which currently remain in moist forest habitats of this State.

Although the existing native forest resource appears to be largely intact (Table 1), detailed assessment of individual populations has never been undertaken. This must constitute a research priority within the proposed management plan. Monitoring of tagged specimens and their source populations will assist in this regard. The absence of effective control and coordination of harvesting to date means that local populations in accessible areas have either been removed already or are increasingly threatened by poaching. Hence the present serious attempt by the Commonwealth and by Tasmania to plan for effective management of this species is decidedly a once-only opportunity for effective conservation of existing populations and natural genetic variation.

This analysis of the physiology and ecological behaviour of *D. antarctica* points cautiously but optimistically towards future directions for sustainable horticultural use of this species. The key will be to ensure that short-term strategies for management of *Dicksonia* harvest are used to promote and implement long-term protection and understanding of native forest populations.

We suggest that light, moisture and nutrient requirements of *Dicksonia* can be provided adequately in plantation forest understoreys or beneath disturbed native forests, without compromising either the productivity of the plantation or the ecological succession of forest gaps. Techniques for sporophyte propagation of *Dicksonia* from prolific yields of wild spores are well established (M. Garrett, pers. comm.; Goudey & Hill, 1986). *In vitro* propagation of sporophyte tissues also offers promise in relation to cloning and multiplication of isolated or threatened genetic material. This investigation offers cautious prospects for sustainable silvicultural production of advanced adult tree ferns in moist eucalypt forests and plantation understoreys. Properly managed and supported by well-targeted research, the long-term sustainable management of *Dicksonia antarctica* for commercial horticulture seems assured.

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APPENDICES

APPENDIX A. Extracts from Project Proposal

DATE: 16th May 1994.

Re: **Application for Aust. Flora Foundation research grant:**

1. Project Title **Regeneration Biology and Silviculture of Tasmanian Soft Tree Fern *Dicksonia antarctica* .**

2. Short Title **Regeneration and Silviculture of *Dicksonia***

3. Project Duration Three (3) years, 1995-1997 incl.
AFF Support required 1.2.95 - 31.12.97.
Commencement date: 1 st February 1995

4. Total Grant Requested $4200 per year for three years $ 12,600

5. Principal Researcher **Mr Greg. Unwin** B.Sc.(For.) M.Sc. M.ASPP. M.IFA.
Lecturer, Applied Biology (Forest Ecologist & Agroforester,
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LAUNCESTON, Tas. 7250.

6. Other Personnel **Mr Mark Hunt** B.App.Sc.(Hons).
CRC Temperate Hardwood Forestry
University of Tasmania.

7. Location **Applied Biology, Uni. of Tas., Launceston.**
and field sites in northern Tasmania.

APPENDIX B. PROJECT OBJECTIVES

(i) Preliminary investigation of regeneration biology and microclimate requirements for growth of Soft Tree Fern in native moist forest and in clearfelled plantation sites, notably to establish silvicultural requirements of the tree fern as a commercial understorey crop in *Eucalyptus* plantations, presently being widely established by large scale private forest companies in northern Tasmania.

(ii) Development of suitable techniques for nursery propagation, micropropagation, species provenance and site tolerance trials, suitable to complement and progressively to replace existing salvage of mature *Dicksonia* from field harvest, prior to reduction of the private forest clearance programme for plantation establishment.

(iii) Initial silvicultural trials of ***Dicksonia*** **as an undercrop,** specifically to place nursery stock of spore-propagated *Dicksonia* in established *Eucalyptus nitens* plantations of ages 5-18 years, in northern Tas.