ECOLOGY OF THE TOP END BAMBOO

Bambusa arnhemica

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Thesis submitted to meet the requirements of a degree of Doctor of Philosophy (Science).

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Date of submission: ____________________

DECLARATION

I hereby declare that, with the qualification stated below, the work herein submitted as a thesis for the degree of Doctor of Philosophy (Science) at Charles Darwin University is the result of my own investigations, and all references to ideas and work of other researchers have been specifically acknowledged. Two chapters herein have been or will be submitted for publication jointly with Prof. David Bowman. Prof. Bowman's particularly substantial input to these chapters is acknowledged, but does not exceed that appropriate for his supervisory role.

I hereby further certify that the work embodied in this thesis has not already been accepted in substance for any degree, and is not being currently submitted in candidature of any other degree.

3/9/04

Donald Charles Franklin

ACKNOWLEDGEMENTS

For their supervision and/or intellectual and personal support, I am indebted to David Bowman, Peter Whitehead and David Lawson. This research was funded generously by Parks & Wildlife (Northern Territory), who provided a scholarship, an expense allowance, unlimited vehicle mileage and supplementary funding for air surveys. Additional financial and general support was received from the Key Centre for Tropical Wildlife Management at Charles Darwin University. For her patience and support through long periods of field work and and an intense write-up, I am grateful to Christine Maas. Many other people also made invaluable and much-appreciated contributions; these are acknowledged in the appropriate chapters herein.

ABSTRACT

In this study, I aim to provide basic biological and ecological knowledge about *Bambusa arnhemica*, the sole bamboo occurring wild in the Northern Territory of Australia, as a prelude to management considerations.

On the basis of a detailed morphological description, the generic placement, monospecific status, and endemicity of *B. arnhemica* are confirmed. At global and catchment scales, a seemingly idiosyncratic distribution may be explained as the product of infrequent and incomplete dispersal across and away from riparian areas, combined with passive dispersal downstream. At local scales, evidence is provided that *B. arnhemica* is constrained by poor drainage during the dry season, and by the high frequency of fire in the savanna matrix within which it is embedded. However, seedlings cope remarkably well with both fire and prolonged wet-season inundation. *Bambusa arnhemica* is gregariously semelparous, flowering in patches ranging from 0.002 to 3200 km^2. A temporally-ordered but spatially-chaotic flowering wave commenced in 1996, affected *c.* 80% of stands by 2002, and is ongoing. It is proposed that gregarious flowering is initiated by an endogenous clock that usually overrides environmental effects, and maintained by strong selection against asynchrony. Synchronicity is progressively fragmented over generations by occasional environmental effects that induce synchronously early or late flowering without altering the endogenous clock, but renewed with dispersal and speciation.

Bambusa arnhemica is facultatively deciduous. Rapid elongation of culms occurs during the mid- to late- wet season, and must be completed before the onset of the dry season, a trait that may limit *B. arnhemica* to sites where wet-season moisture is prolonged and reliable.

Bambusa arnhemica is neither a recent arrival nor an ancient inhabitant of northern Australia. Gregarious occupation of space and gregarious flowering by semelparous bamboos provides intriguing perspectives on the conundrum of group *cf* individual selection. Clumping bamboos are ideal subjects for intensive management and harvest, but pose unusual problems for harvest from wild stands.

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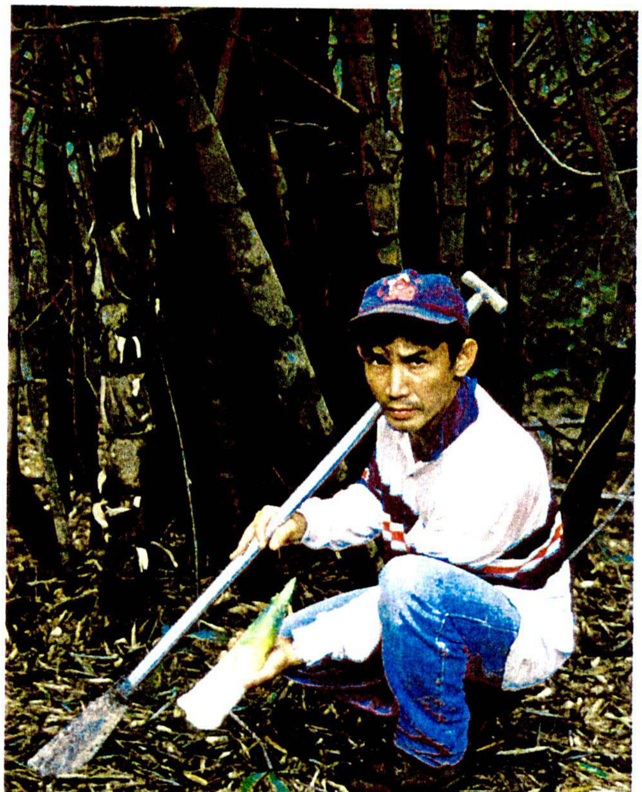
Introduction: ignorance is bliss?



Didgeridoo photo courtesy of Guan Lim.

The starting point for this thesis was one of quite remarkable collective ignorance. Notwithstanding an almost voluminous literature on the vegetation of the Top End of the Northern Territory, much and perhaps most of it from studies in the north-west where the riparian vegetation that often contains *Bambusa arnhemica* occurs, riparian vegetation scarcely features, and that in which *B. arnhemica* occurs not at all. Prior to this study, the few recent references to the species in the scientific literature were all somewhat incidental and related to faunal use (Palmer & Woinarski 1999; Tidemann *et al.* 1999; Woinarski *et al.* 2000).

Although officially treated as an endemic, native species (Liddle *et al.* 1994; Mallett & Orchard 2002), there was no basis for such an assumption, and locally it is regarded by some as an exotic and pestiferous species. Its affinities, even to the level of generic placement, had never been rigorously assessed (but see Muller 1997). In his formal original description, Mueller (1886) raised the possibility that bamboo stands in the Top End comprised more than one species, doubts that have been repeated (Bindon 1991; Spencer 1986) but never resolved.

But at least, one might have thought, one could infer much about bamboo ecology and management from the voluminous overseas literature. Hardly so! Since the classic works on bamboo horticulture (Ueda 1960) and biology (McClure 1966), the bamboo literature has contributed remarkably little from which direct inference about *B. arnhemica* could be made.

The most substantial body of ecological study of bamboo has undoubtedly been undertaken in temperate Japan on leptomorph species in the genera *Phyllostachys* and *Sasa*. The leptomorph or running growth form differs fundamentally from the pachymorph (clumping) form of *B. arnhemica* and other tropical species, corresponding to the contrasting "guerilla" and "phalanx" growth strategies amongst clonal plants (Lovett Doust 1981). The growth forms also correspond to a primary phylogenetic difference, thought to represent an initial or very early branching of the tribe Bambuseae (the woody bamboos) (Watanabe *et al.* 1994, Kobayashi 1997). Given the importance of bamboo as a resource in Asia (Rao & Rao 1995), the demographic consequences of the removal of shoots or culms remain virtually undocumented beyond a few generalisations such as that over-harvest and selective harvest of larger culms causes degradation of clumps (e.g. Ueda 1960, Banik 1997). Although wild bamboo stands are quite extensively exploited in many parts of the world, published management options appear inappropriate to the Northern Territory setting. For example, Prasad (1985) and Banik (1990) deal with issues arising from intense exploitation of bamboo forest ecosystems during the bamboo regeneration phase, whilst Azmy *et al.* (1997) and Ding JianLin *et al.* (2000) focus on intense silvicultural practices such as active thinning, removal of competing vegetation and application of fertiliser. The evolutionary and ecological significance of mass-flowering and semelparity in bamboos remain speculative and contested (Janzen 1976; Gadgil & Prasad 1984; Campbell 1985; Keeley & Bond 1999, 2001; Saha & Howe 2001), whilst the molecular mechanisms involved remain "basic biological mysteries" (Judziewicz *et al.* 1999).

The relevant aspects of bamboo biology and ecology are reviewed in the introduction to each chapter, so will not be repeated here. But what do we know about *B. arnhemica* and bamboo in Australia?

Bamboo in Australia

> "Most Asian countries treat this fastest growing, annually renewable, resource with great reverence. Bamboo feeds them, houses them, graces and shades their environment. It is used to make their musical instruments, cooking and eating utensils, furniture, hunting weapons, and ceremonial artifacts. It even provides ...." (Cusack 1999)

With only three or possibly four species of woody bamboo, and these confined to relatively remote areas of the tropics (Fig. 1), Australia is both biogeographically and psychologically marginal to the great Asian centres of bamboo diversity and culture. In dramatic contrast, a 900 km^2 forested region of southern China is estimated to contain 144 naturally-occurring species (Bystriakova *et al.* 2003).

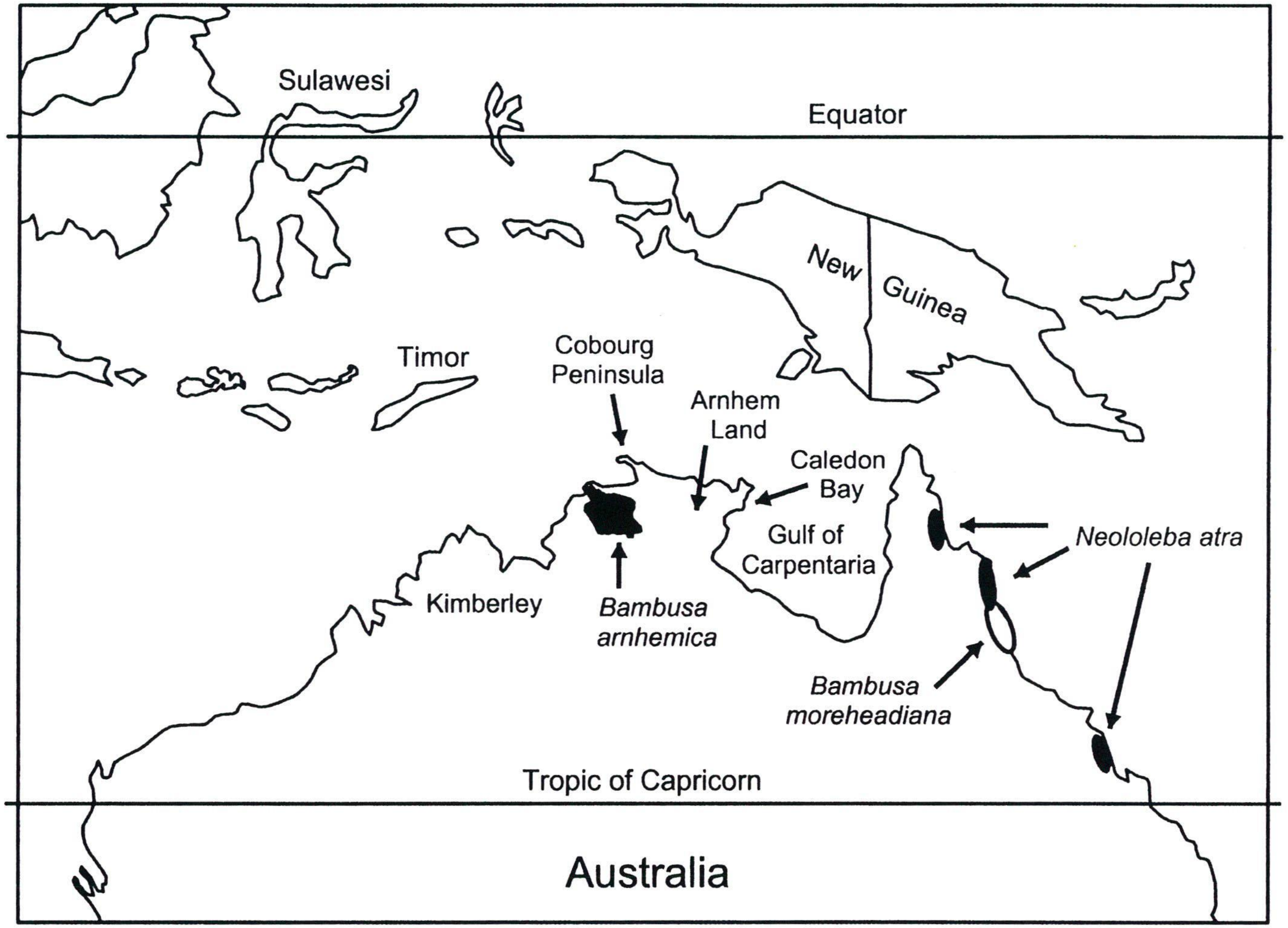


Figure 1: Northern Australia, Papua New Guinea and nearby parts of the Indonesian archipelago, showing locations referred to in the text and the natural distributions of woody bamboos within Australia.

Bamboo distributions modified from Liddle *et al.* (1994) and Mallett & Orchard (2002). Map prepared by Dan McIntyre.

Reinforcing this marginality in Australia, there are no known bamboo-endemic vertebrates in Australia, perhaps the nearest being the White-browed Robin *Poecilodryas superciliosa*, the Buff-sided subspecies *cerviniventris* of which displays a non-obligate preference for stands of *B. arnhemica* (Woinarski *et al.* 2000). Schodde & Mason (1999) proposed elevating ssp. *cerviniventris* to specific status. Possible invertebrate associations with bamboo in Australia are unknown. A leaf-spot fungus of uncertain taxonomic status was described from *Bambusa arnhemica* by Pearce *et al.* (2000). In the case of *B. arnhemica*, it is unclear whether the lack of an endemic fauna reflects relative recent arrival in Australia or the effects of the severe Pleistocene squeeze on the diversity of fauna restricted to moist environments in the Northern Territory (Bowman & Woinarski 1994; Franklin & Noske 2000). However, the bamboos of the wet tropics in Queensland are less likely to have suffered such an effect. In marked contrast, bamboo-endemic fauna are well-known in a number of other regions, for example, several species of lemur in Madagascar (Tan 1999), two species of panda in Asia (Carter *et al.* 1999; Wei *et al.* 2000; Pradhan *et al.* 2001), and a diversity of rodents and birds in South America (Stallings *et al.* 1994; Kratter 1997). Judziewicz *et al.* (1999) lists 93 species of birds endemic to bamboo understoreys in South America, and at least one more has been discovered since (Lentino & Restall 2003).

All three mainland Australian woody bamboos were initially placed in *Bambusa*. *Bambusa forbesii* was long considered to be restricted to New Guinea (Holttum 1967) and the Iron Range in north Queensland, but recent surveys have extended its known distribution south to the Cairns and Mackay regions (Mallett & Orchard 2000). On the basis of its simple branching system (a key trait in bamboo taxonomy), Widjaja (1997) transferred it to the genus *Neololeba*, and in the process reduced it to synonymy with the widespread Indonesian species *N. atra*, the latter name taking precedence. *Bambusa moreheadiana* is a climbing bamboo believed endemic to the core wet-tropical region centred on Cairns in north Queensland (Mallett & Orchard 2000). Its placement in *Bambusa* has been contested (Muller 2001), but suggestions that it is a *Dinochloa* (Cusack 1999), a genus of climbing bamboos, are incorrect based on pseudospikelet structure (Clifford 1993). A fourth Australian species has tentatively been identified from Murray Island in Torres Strait and even more tentatively attributed to the genus *Schizostachyum* (Cusack 1999). These evident differences suggests that bamboo may have colonised Australia from Asia on four separate occasions (Franklin 2003). But we do not know how long bamboo has been in Australia.

History of *Bambusa arnhemica*

The Indigenous people of northern Australia made considerable use of *B. arnhemica*, principally as spear shafts but also for production of didgeridoos, long-stemmed smoking pipes, ceremonial frames, water carriers, wood-carving chisels and rafts (Tindale 1925; Bindon 1991; Marrfurra *et al.* 1995; Blake *et al.* 1998, G. Wightman pers. comm.). The light weight of spears with bamboo (*cf* wood) shafts was advantageous in several situations. They were preferred for fishing by the Wardaman people (Raymond *et al.* 1999) though not those of eastern Arnhem Land (Tindale 1925). In war, the light weight of bamboo-shafted spears enabled more weapons to be carried, and the join between the shaft and the heavier spear-head meant that the spears broke on impact, precluding re-use by the enemy (Tindale 1925). Bamboo was traded extensively east into Arnhem Land, and south and south-west from the Daly River area as far as the Kimberley (Figs. 1,2) (Thomson 1949; Berndt & Berndt 1988, G. Wightman pers. comm.). The Balamumu people from Caledon Bay on the east Arnhem coast, 420 km east of the distributional limit of *B. arnhemica* stands (Liddle *et al.* 1994), specialised in the production of bamboo fighting spears (Tindale 1925). Curiously, I can find no written record suggesting Aboriginal use of either bamboo culm shoots or seed as food. The Wagiman people near Pine Creek used the shoots for food, but the practice was evidently not widespread and may be of recent, Chinese origin (Glenn Wightman pers. comm.).

A plausible but hypothetical case has been made that Aboriginal people could have reached Australia on bamboo rafts (Flood 1995, Bednarik *et al.* 1999). However, evidence from Aboriginal usage that *B. arnhemica* may have been in the region for millennia is frustratingly elusive. Usage and cultural value need to be interpreted in the light of the demonstrable ability of Aboriginal people to rapidly adopt novel foods into traditional diets and culture, as demonstrated with the fruit of the Tamarind *Tamarindus indica* (Mitchell 1995) and meat of Water Buffalo *Bubalis bubalis* (Bowman & Robinson 2002). Remains of bamboo have been detected in archaeological deposits in Kakadu National Park, but only in deposits no more than, and possibly much less than *c.* 800 years of age (Clarke 1988). The lack of earlier records may reflect that bamboo does not last long in this situation (Annie Clarke pers. comm.). Surprisingly, there is only one possible representation of bamboo in the extensive Arnhem Land Plateau rock art record, that of a man playing a didgeridoo (Chaloupka 1997, p189). The didgeridoo is banded, which may be merely decorational or could represent bamboo nodes. The painting is only a few hundred years old (Pina Giuliani pers. comm.). The persistence and detectability of

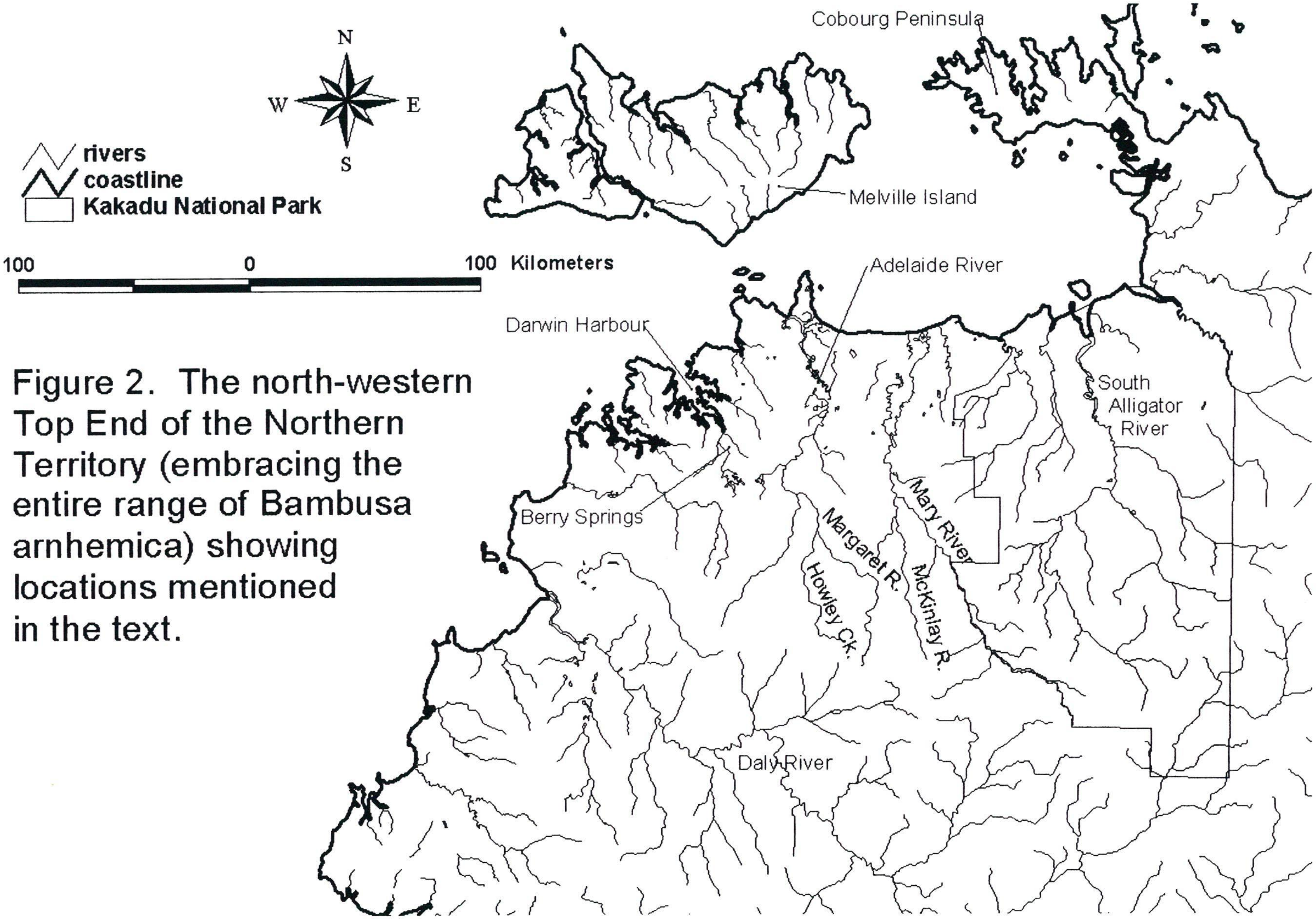


Figure 2. The north-western Top End of the Northern Territory (embracing the entire range of Bambusa arnhemica) showing locations mentioned in the text.

bamboo residues on stone tools (Jahren *et al.* 1997) offers some prospect for further exploration of the issue.

The popular notion that Macassan trepangers introduced *B. arnhemica* from Sulawesi or nearby islands (Fig. 1) to northern Australia in the 18th or 19th centuries (White 1971) is not supported by the presence of live bamboo at Macassan camp sites or nearby springs. In contrast, the introduced Tamarind tree *Tamarindus indica* is commonly associated with these situations (Macknight 1976; Bindon 1991; Mitchell 1995). Furthermore, because trepang is most abundant in clear water, the major trepanging grounds in northern Australia were off rocky rather than mangrove-lined coasts. Thus it was that Macassan camp sites were concentrated from Cobourg Peninsula east to the Gulf of Carpentaria, and along the Kimberley coast in the west (Macknight 1973, 1976), a distribution that almost perfectly excises the coast adjacent to which *B. arnhemica* is found (Bindon 1991; see also Chapter 3).

There can, however, be no doubt that *Bambusa arnhemica* was well-established within its current distribution prior to European settlement, as early European explorers reported it from locations where it is known to this day (Table 1, Fig. 2).

Table 1. Some early European records of *Bambusa arnhemica*.

Year	Explorer	Location	Source
1839	John Lort Stokes	Talc Head, Darwin Harbour	Stokes (1846)
1845	Ludwig Leichhardt	South Alligator River	Leichhardt (1847)
1862	John McDouall Stuart	Mary and Adelaide Rivers	Stuart (1865)
1866	John McKinlay	Margaret, McKinlay, Mary and tributaries of the South Alligator River	McKinlay (1866)

Bambusa arnhemica was described for science by Baron Ferdinand von Mueller in 1886 from specimens sent to him by Moritz (Maurice) Holtze from the Daly River. The description includes both flowers and foliage (*contra* Soderstrom & Calderon 1979; Spencer 1986; Ohrnberger 1999), but the rhizome, culm, culm sheath, branch structure and seed were not described, a situation only partially rectified by subsequent work (Cowie *et al.* 2000; Muller 2002).

Since Mueller's description and until quite recently, reference to *B. arnhemica* in any biological, ecological or horticultural context was remarkably infrequent. Dahl (1926) encountered "heavy bamboo jungles" and "thick bamboo" on the Daly River and its tributaries, and described the rapid elongation of culms during the wet season: "After a few days' rain with following sunshine, one might see shoots which previously had been only just visible stand more than a yard high" (page 164). Conigrave (1936) photographed a "bamboo jungle" on the Adelaide River.

A recent general increase in interest in bamboos for horticulture within Australia and other non-bamboo cultures has spawned a number of mostly brief references to *B. arnhemica* but little of substance. Attempts at horticulture in temperate regions have yielded the information that the species is "very frost tender" (Elliot & Jones 1982), Cusack (1999) suggesting that it is intolerant of temperatures below 5°C. Spencer (1986), Bindon (1991) and Muller (1997) provided general overviews of the Australian bamboos.

Bambusa arnhemica has featured in a number of local plant identification guides (Clarke & Traynor 1987, Brock 1993, Cowie *et al.* 2000). Liddle *et al.* (1994) documented the distribution of the species based on records of the Darwin Herbarium and the rainforest survey of Russell-Smith (1991), showing that it is largely restricted to the area from Kakadu National Park west and south-west to the Daly River and north to Melville Island.

Recent utilization of *B. arnhemica*

Lazarides (2002) noted that *B. arnhemica* has been "used in outback settlements as windbreaks, garden fences, stakes and for the insulation and walling of shade houses and small outbuildings". It has been used sporadically as a specimen plant in Darwin gardens for at least fifty years (Hearne 1975; Muller 2002), though its tendency to thorniness limits its desirability. Recently, culms have been harvested for the commercial production of cheap didgeridoos. However, the major story of recent utilization relates to the harvest of culm shoots for food.

One can readily imagine that use of *B. arnhemica* culm shoots commenced with the migration of Chinese to the Northern Territory goldfields in the 1870s and 1880s, though I can find no direct evidence of it. There is considerable overlap between the goldfields mined by the Chinese and the distribution of *B. arnhemica*, notably in the area of the upper McKinlay and upper Margaret Rivers and Howley and Bridge Creeks, including the still active Mt Wells and Brocks Creek Mines (Jones 1990). The Chinese population persisted after the initial gold rush, and has become a prominent part of the Northern Territory community. Laurence Ah Toy (pers. comm.) recalled family excursions to Coomalie Creek in the 1950s to harvest bamboo shoots for their own use, and that a mass-flowering and die-off event in that period rendered shoots unavailable. During the 1970s, there was a dramatic rise, in both proportional and absolute terms, in migration of people from the bamboo cultures of Asia to the Northern Territory (Skinner *et al.* 1994), and there is little doubt that recent interest in the harvest of bamboo shoots from wild stands of *B. arnhemica* has been driven substantially by this migration wave.

Larger-scale commercial harvest from wild stands of *B. arnhemica* emerged as an issue in the mid- to late- 1990s. Considerable illegal harvest activity was detected by staff of the then Parks & Wildlife Commission of the Northern Territory in 1997 (David Lawson pers. comm.). Cusack (1999) reported "some tonnes" of *B. arnhemica* shoots being sold on "markets", presumably in southern and eastern Australia, in 1998. Under the *Territory Parks & Wildlife Conservation Act*, a permit is required for commercial (but not non-commercial) harvest of shoots from wild bamboo stands whether on private or public land, with a royalty payable for harvest on public (including leasehold) land (Robert Taylor, pers. comm.). A number of commercial licenses for the harvest of *B. arnhemica* shoots from the wild were issued in 1997 and 1998, but none in 1999. Official returns demonstrate that the legal harvest never achieved the level of "tonnes".

These developments coincided with the emergence of a bamboo plantation industry within Australia (Midmore 1998; Cusack 1999, 2002) including the Northern Territory (Wood 2001, Kyle 2002). Grower attitudes to the harvest of wild shoots varied from broadly supportive to quite antipathetic. Concerns that an aperiodic supply of wild shoots resultant from the dumping of illegally-obtained shoots was causing extreme fluctuations in market price, and that poor pre- and post-harvest practices were giving the (NT) shoot industry a bad name, may have had some justification. *Bambusa arnhemica* shoots can be quite palatable and may have novelty value as bush tucker (Wood 2001), but are often regarded as somewhat inferior to those of premium bamboos of Asian origin. Cusack (1999), however, described *B. arnhemica* shoots sold at the markets as "inferior, bitter, scruffy-looking". Concerns that the Australia New Zealand Food Authority might ban the sale of fresh bamboo shoots because of the cyanide levels sometimes reported in *B. arnhemica* shoots have not been realised. Allegations that the harvest was taking place within Kakadu National Park appear without foundation, the major harvest areas being along the Adelaide and lower Mary Rivers (Fig. 2).

One Northern Territory grower, Phil Vivian, has established a commercial plantation of *B. arnhemica* as part of a larger horticultural development near Berry Springs (Kyle 2002). Shoots are harvested twice-weekly during peak season and sold on southern markets (P. Vivian pers. comm.). Appropriate management regimes are being developed by trial and error from known management practices applied to other commercial varieties, and with reference to the results of an Australian Centre for International Agricultural Research project being conducted on the property. Current agronomic research at the Coastal Plains Research Station aimed at optimising shoot production in *Dendrocalamus* spp. may also be applicable to plantation *B. arnhemica* (Mark Traynor pers. comm.).

As a strategy for combining economic development with conservation, sustainable utilization of wildlife is encouraged in the Northern Territory (PWCNT 1995). However, the sustainability of commercial-scale harvests of wild *B. arnhemica* is unknown. Concerns about an expanding commercial harvest were seriously compounded when mass-flowering of *B. arnhemica* along the tidal section of the Adelaide River in 1998 abruptly rendered substantial areas unavailable for harvest, increasing pressure on the remaining stands. Furthermore, whether the harvest could have consequences for the flowering and subsequent regeneration of other stands, and whether these other stands were due to flower in the coming years, was also unknown. It is in this context that Parks & Wildlife (Northern Territory) placed a temporary ban on all commercial harvest, and funded the research program of which this thesis is part.

Aims and layout of thesis

Notwithstanding the management imperative driving this study, this thesis comprises five chapters focussed on biological or ecological issues, along with a brief general discussion. Data and observations more directly relevant to management, including the results of two harvest trials, along with a considerable body of demographic data, will be analysed subsequently and presented elsewhere. The aim here is to provide background biological and ecological information on which more specific management research and recommendations may subsequently be built. A substantial general ecological component to the project was agreed at the outset with Parks & Wildlife staff (David Lawson and David Cheal), and is an acknowledgement that management of wild populations can scarcely occur in a vacuum of biological and ecological knowledge as comprehensive as that facing us with *B. arnhemica*.

Each of the five core chapters is written as a manuscript in form for direct submission to journals. Two have already been published, and the remainder submitted. As each chapter begins with a self-contained introduction and ends with a self-contained discussion, this Introduction is general in nature. In Chapter 2, I deal with the outstanding taxonomic questions about the status and endemicity of the taxon, the management implications of which are far-reaching – the difference between dealing with an exotic pest and a restricted-range endemic. In that chapter, I also provide a detailed morphological description which underpins all subsequent chapters, and most especially the yet-to-be-analysed demographic data. Chapters 3 and 4 deal with *B. arnhemica*'s position in the landscape, Chapter 3 from an extensive, whole-of-range perspective and Chapter 4 by intensive study of two nearby but contrasting sites. In Chapter 5, the mystery of bamboo flowering patterns is explored through a landscape- and local-scale study of spatio-temporal patterns. The simple description of these patterns has enabled me to generate an hypothesis for their development which reconciles the conflicting perspectives brought about by emphasis on either the synchronous and asynchronous elements of bamboo flowering patterns. In Chapter 6, I explore the relationship between seasonal patterns of growth and the monsoonal climate, and how the unique form of bamboos provides opportunities and limitations for dealing with climatic regularities and vagaries.

For centuries and probably millennia, *B. arnhemica* has been utilized by the Indigenous people, and the absence of a Western scientific perspective on the species was of no concern. The same may be said of the more recent utilization of culm shoots for local consumption in the presence of only a small human population. In the absence of real pressure on the bamboo population, scientific ignorance can truly be said to have been blissful. But with the emergence of a commercial harvest, this is no longer so. There are parallels overseas, particularly in Asia, where for centuries the bamboo cultures have co-existed with bamboo forests and plantations, doubtlessly having acquired the folk knowledge to more-than-satisfactorily manage the resource. But in the face of rapid population expansion during the 20th century, compounded in some cases by the commercialisation of bamboo such as for the production of paper in India, Asia too needs the new management tools that science can provide (Fu Maoyi & Banik 1995, Rao & Rao 1995). Scientific ignorance is no longer bliss!

In two other very real senses, though, ignorance *was* bliss. Had I realised the complexity of the issues to be dealt with, I might not have undertaken this study, but I have no regrets about having done so. And our collective ignorance has given me a unique opportunity to address fascinating and rewarding basic biological and ecological questions that have implications for both the Australian monsoon tropics and bamboo beyond our shores.

Acknowledgements

David Bowman, Glenn Wightman, Mark Traynor and Phil Vivian provided helpful comments on a draft of this chapter. Dan McIntyre provided extensive assistance with the drafting of Figure 1.

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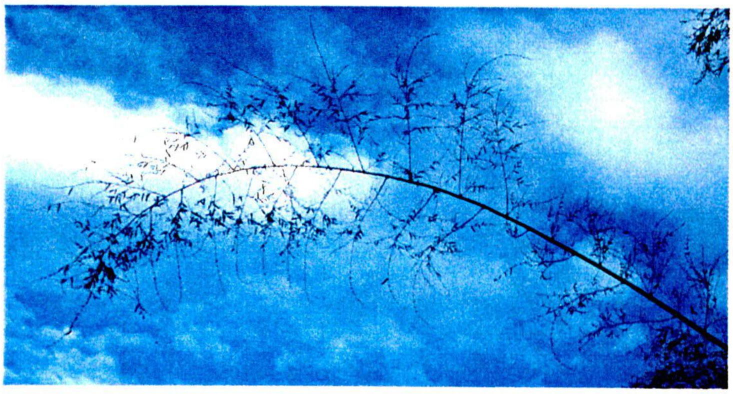
Chapter 2:

Morphology and taxonomy

This chapter has been published as:

Franklin DC. 2003. Morphology and taxonomy of the Top End Bamboo *Bambusa arnhemica* F. Muell., a little-known bamboo from northern Australia. *Bamboo Science and Culture* 17: 44-54.



Abstract

The first comprehensive morphological description of *Bambusa arnhemica*, a little-known species from the monsoonal tropics of northern Australia, is provided. *Bambusa arnhemica* is a medium-sized, pachymorph, unicaespitose and thorny bamboo. Its affinities remain unclear, although its inclusion in *Bambusa* is confirmed on the basis of a range of traits including the pseudospikelet, floret, caryopsis and thorny basal branches. Features of the species include: culm sheaths that lack auricle lobes; trimerous, thorny basal branches that contrast with the thornless, unrestricted branch complements of the upper culm; slender, rigid thorns that rarely give rise to leafy shoots; the formation of caducous leaf-like inflorescence bracts immediately prior to flowering, and culm shoots of highly variable colour. No synonymous Australian or Asian species could be identified, and it is concluded that *B. arnhemica* is endemic to Australia.

Introduction

Since being named late in the 19th century (Mueller 1886), the northern Australian bamboo *Bambusa arnhemica* F. Muell. has received remarkably little scientific attention. Its has not been described adequately, its affinities are unknown, and Soderstrom and Calderon (1979) queried its placement in *Bambusa*. The suggestion that more than one species of bamboo may occur within the area occupied by *B. arnhemica* was made as a footnote to the original description (Mueller 1886) and has never been formally addressed or resolved (but see Muller 1997). Although Mueller described it as an endemic species, and this is the official position (e.g. Liddle *et al.* 1994, Cowie *et al.* 2000), the notion has never been formally examined. Indeed, it is popularly held by some to be a recent introduction to northern Australia from Asia, perhaps transported by Macassan trepangers, though Macknight (1976) refuted the latter suggestion, pointing out that *B. arnhemica* is not associated with Macassan camp sites along the northern Australian coast.

Mueller's description was of less than 200 words and the species was not illustrated. However, fertile as well as vegetative material was described, contrary to suggestions by Soderstrom and Calderon (1979), Spencer (1986) and Ohrnberger (1999). Cowie *et al.* (2000) illustrated leaves, the flowering branch, spikelets, lemma, palea and seed, and Muller (1997) illustrated culm sheaths. However, the rhizome, branch bud, branching pattern and culm shoot, structures fundamental to bamboo taxonomy, remain to be described.

Bambusa arnhemica is thought to be endemic to the sparsely-populated, monsoonal tropical "Top End" of the Northern Territory, Australia. It is largely confined to watercourses (Fig. 1*a*) embedded in the wooded savanna environment of the high rainfall (1,200 – 1,800 mm mean annual rainfall) north-western portion of the region (Fig. 2), where it commonly occurs as a mono-dominant or co-dominant in riparian forest or vine-thicket. Much less frequently, it occurs in non-riparian vine-thicket on rocky hillsides (Fig. 1*b*) and coastal headlands. It has a very limited and recent history in cultivation (Hearne 1975, Cusack 1999, Wood 2001). In this paper, I provide a morphological description of the taxon, recent partial mass-flowering rendering both vegetative and flowering material available. This information is then applied to a consideration of its generic placement and endemicity. These notes and data are intended to provide context for further studies into the ecology, management and biogeographic history of the taxon.

a.

b.

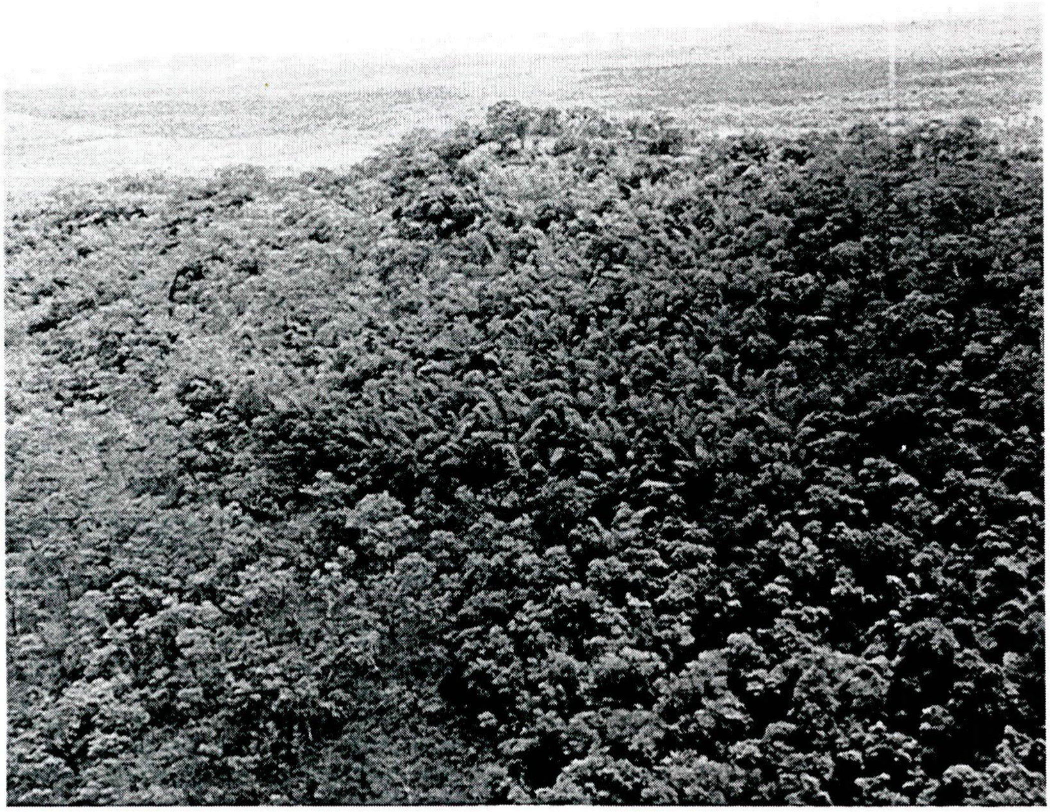


Figure 1. Natural occurrences of *Bambusa arnhemica* in northern Australia: *a.* mono-dominant riparian stand, Mary River; *b.* deciduous vine-thicket stand on rocky hillside, Mt. Paqualin.

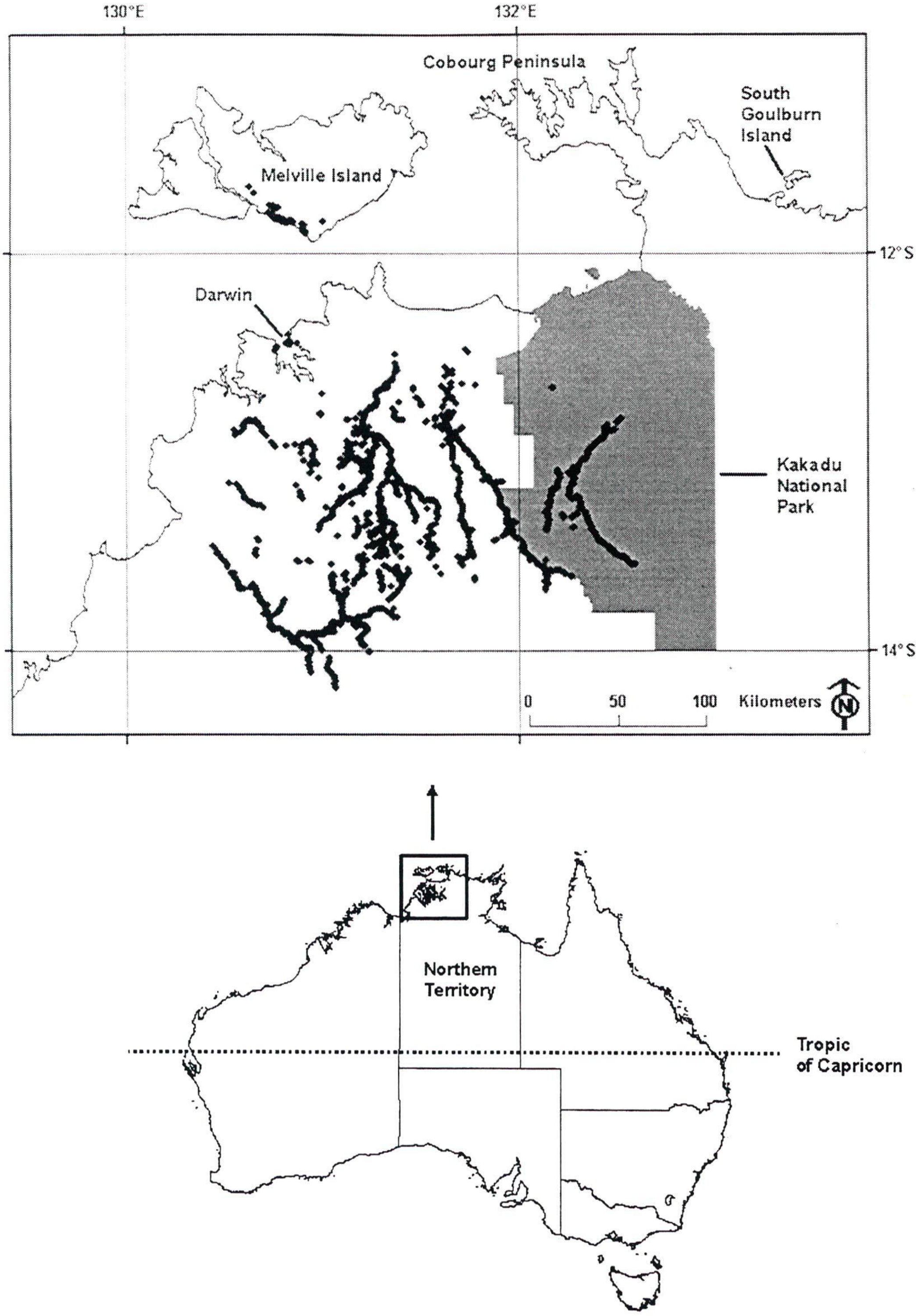


Figure 2. Distribution of *Bambusa arnhemica* (black dots), based on 1601 locations identified by the author during ground, boat and air surveys.

Note the predominance of linear stands, which are associated with watercourses. Map prepared by Daniel McIntyre.

Methods

This description is based on an examination of leafy and flowering clumps throughout the range of the taxon, combined with more detailed, site-specific observations. Vegetative material and data were mostly obtained from Mary River Park (12°55'S, 131°39'E). Inflorescence and flower structure is described from fresh collections from Mt Bundy Station (13°14'S, 131°08'E) on the Adelaide River, as well as observations elsewhere in the Adelaide River catchment. Clump heights were measured with a clinometer and tape measure at the 22 of 38 sites selected for study of environmental attributes (to be reported elsewhere) at which there had been no recent mass-flowering. The 38 sites were widely dispersed throughout the range of the species, but the strong spatial aggregation of flowering (in prep.) has unavoidably structured the spatial availability of sites with vegetatively-mature clumps.

Culm dimensions were measured at Mary River Park. The large sample of diameters were measured with a diameter tape at the middle of the internode nearest 1.3 m above the ground. Every culm of 39 clumps in a 90 m long by 15 – 25 m wide riparian stand on the fringe of a billabong (stranded meander) of the Mary River selected for a detailed demographic study (to be reported elsewhere) was measured except that six waterside clumps were excluded for safety reasons, the billabong being inhabited by Saltwater Crocodiles *Crocodylus porosus*. Three fully-developed culms from separate clumps, selected for intactness and accessibility (the latter a substantial constraint), were felled. For each internode, the culm diameter and internode length were measured to 0.1 cm. Every fifth internode was then cut, the wall thickness measured to 0.1 mm using Bergeon vernier callipers at three points, and the results averaged.

Seed was collected at six sites in the upper tributaries of the Adelaide and Daly River systems in November 2000, the samples mixed thoroughly and then sub-sampled. After removal of the lemma, palea and rachilla, seeds were weighed air-dry to 0.1 mg on Sartorius scales, and measured to 0.1 mm using Bergeon vernier callipers, oven-dried for 24 hours at 70°C and weighed again.

In the description of branching orders, the culm is considered to be order zero.

Description

<u>Habit</u> A terrestrial, clumping, bamboo, rarely epiphytic (Franklin 2003); (10–) 12–18 (–21) m tall (Fig. 3*a*), with fewer than 10 to more than 100 live culms, often compact and unicaespitose (Fig. 4) but sometimes open and/or clumps not always distinguishable; facultatively deciduous.

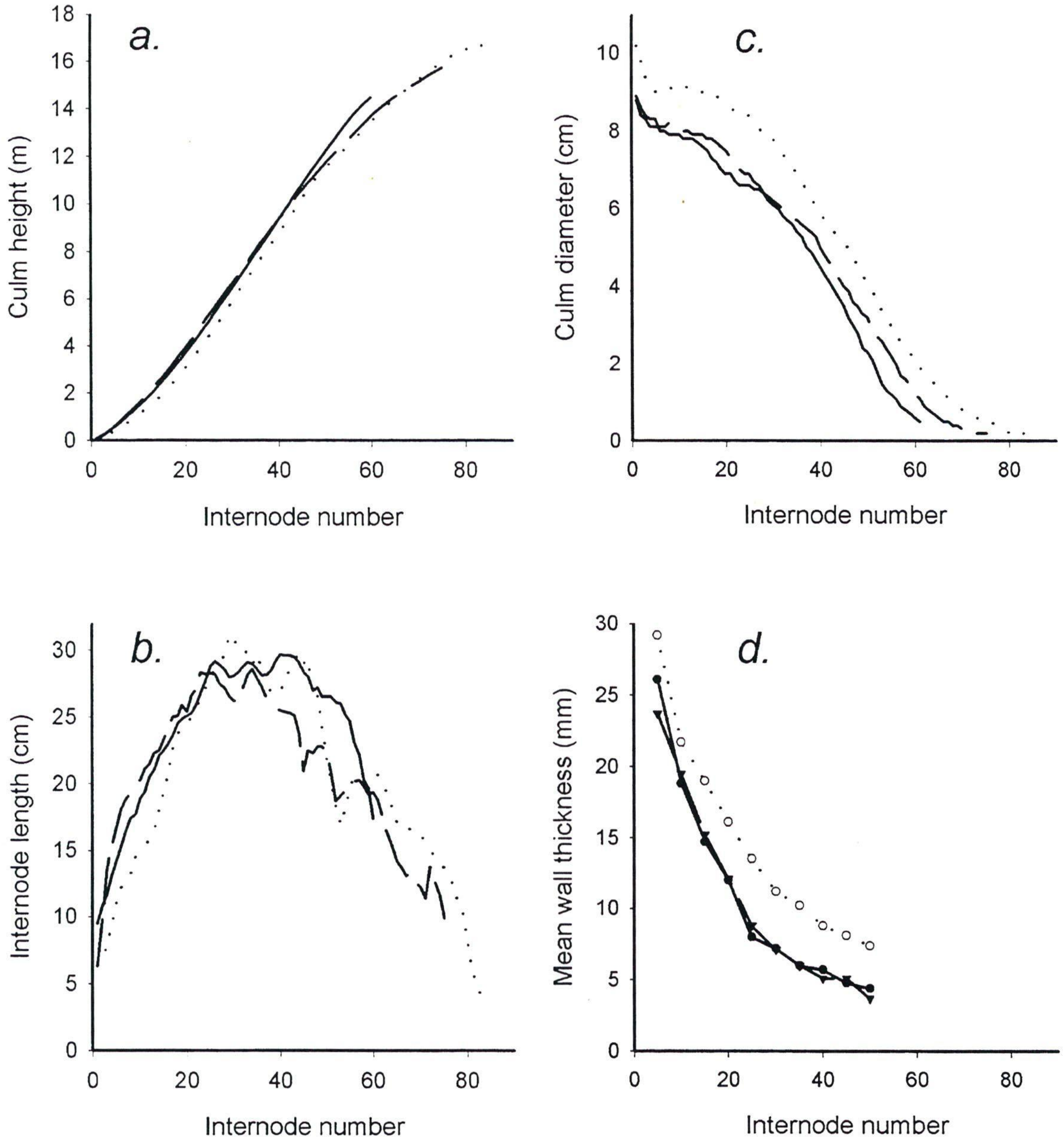


Figure 3. Dimensions of three *Bambusa arnhemica* culms at Mary River Park.

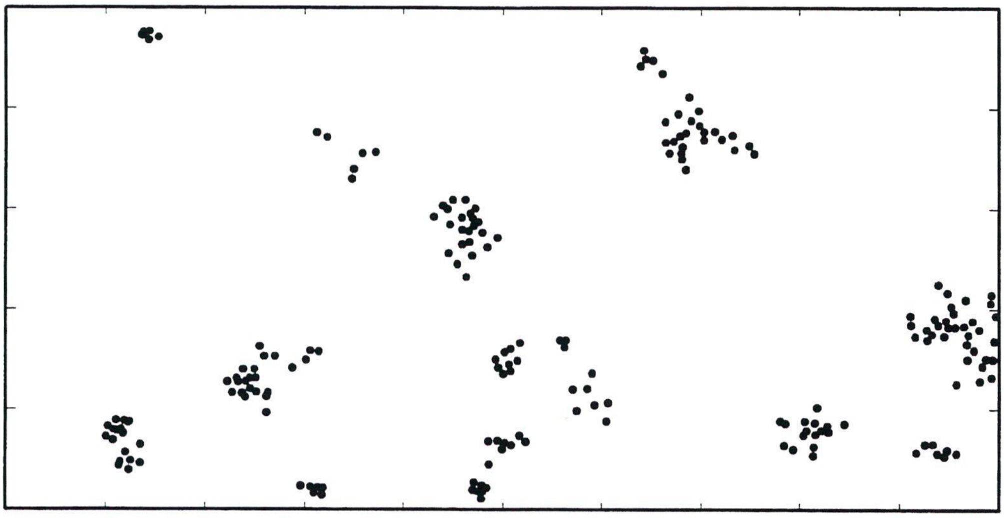


Figure 4. Position of bases of the 201 live *Bambusa arnhemica* culms present in a 20 x 10 m plot positioned in a dense, mono-dominant stand of small clumps on level ground in the vicinity of Finniss River (12°50'S, 130°38'E).

Rhizome Short-necked pachymorph; to 30 (–40) cm long by 10 cm in diameter, sub-fusiform, slightly dorso-ventrally compressed, broadest a short distance below the culm base (Fig. 5*h*). Primary roots to 4 mm diameter.

Culm Erect and straight when young but for the somewhat arching slender tip, or somewhat zig-zag on young clumps, arching progressively with age sometimes to the ground; (3–) 6–8 (–13) cm diameter at 1.3 m, or less when damaged or stressed, highly variable within (e.g. Fig. 6) and between sites, tapering progressively from ground level (Fig. 3*c*), hollow; walls to 3 cm thick (Fig. 3*d*). Nodes to more than 80 per culm (Fig. 3); sheath scar prominent and slightly expanded above the internode to form a collar around the derived internode, depressed below the branch buds; supra-nodal ridge generally absent but may be present on smaller branches; branch buds present at all nodes; lower nodes often bearing root primordia which may develop into a mat of aerial roots to 5 cm long. Branch buds solitary, broadly triangular to obcordate, to 37 mm tall by 54 mm wide; prophylla united, with lateral wings sometimes fringed with hairs on each side (Fig. 5*d*). Internodes glabrous, or with scattered silky hairs when young, cylindrical, almost circular in cross-section, smooth, uniformly darkish glossy green or sometimes glaucous on young culms and becoming olive-green with age, to 30 (–43) cm long (Fig 3*b*), longest just below the mid-culm. Culm shoots variously shiny mid-green, dull pale green, dull pale green tinged maroon, or violet-grey (Fig. 5*i*).

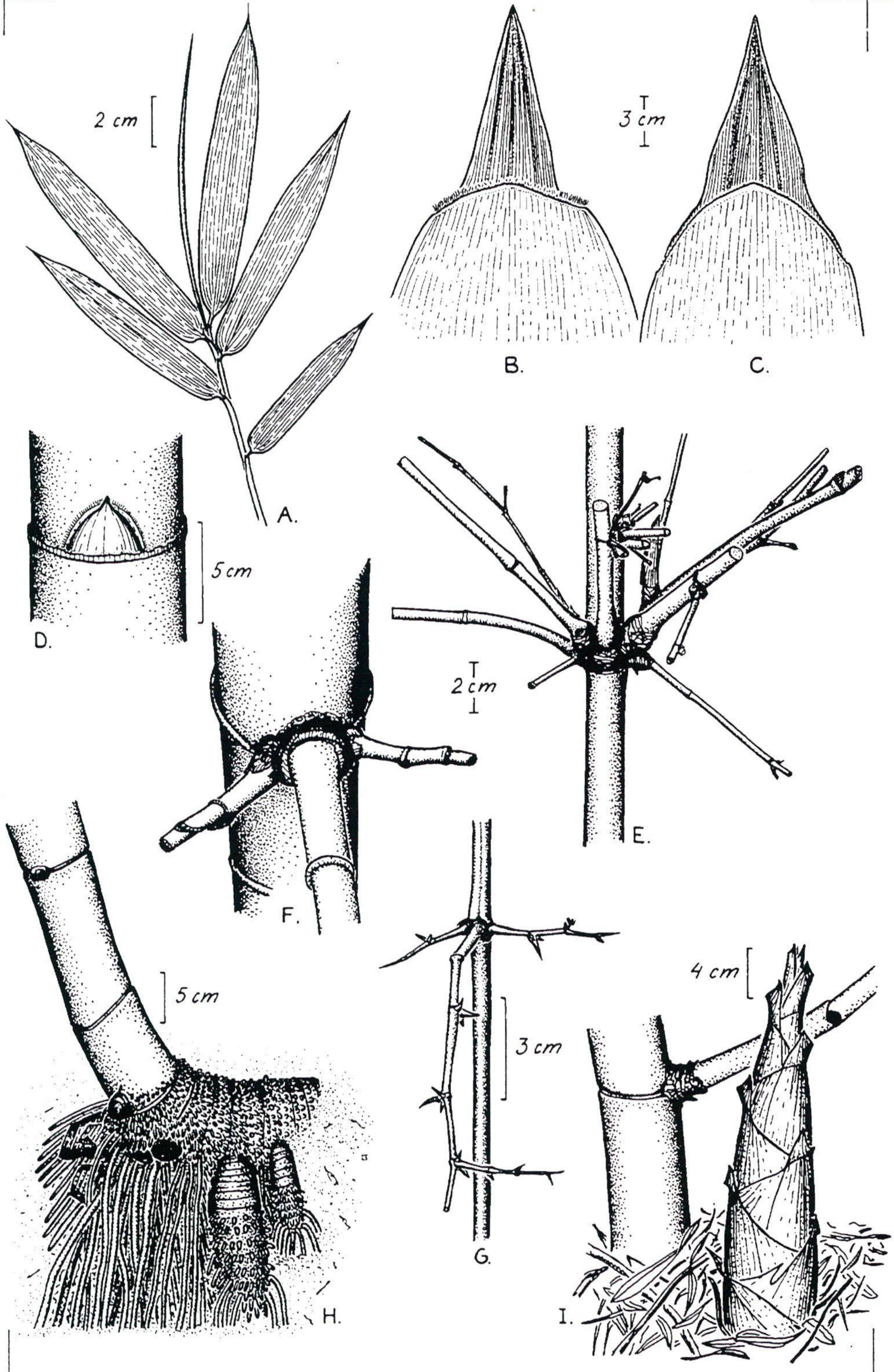


Figure 5. ***Bambusa arnhemica*****:** ***a.*** **leafy shoot;** ***b., c.*** **culm sheath and blade variants;** ***d.*** **branch bud;** ***e.*** **upper branch complement;** ***f.*** **lower branch complement;** ***g.*** **section of lower branch with thorns;** ***h.*** **rhizome and lower culm;** ***i.*** **culm shoot.** Illustrations prepared by Monika Osterkamp Madsen.

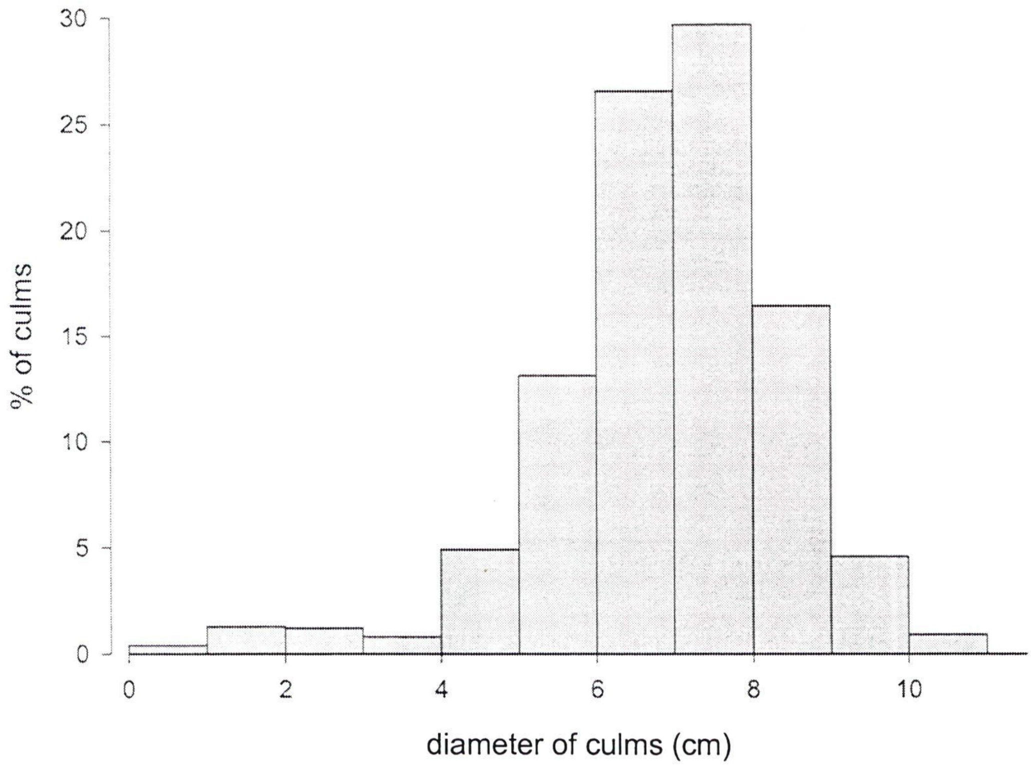


Figure 6. Culm diameters of *Bambusa arnhemica* at Mary River Park.
N = 1219 culms from 39 clumps; culms measured at the internode nearest 1.3 m above the ground.

Culm sheath To 30 (–38) tall by 30 cm across the base, arched-convex at apex, glabrous or almost so when mature, or with minute, pale hairs when young, striate with fine converging (sub-parallel) venation, drying to a thick, papery texture smooth on the inside and corrugate on the outside, varying little in form along the length of culm, mostly shed shortly after culm elongation but lower sheaths persist for up to several years. Ligule scarcely developed to 5 mm long, forming a low curved or sometimes a higher and pointed arch, stiff, sometimes with stiff bristles to 1 mm long in the middle. Blade erect, narrowly triangular, to 15 cm tall by 5.5 (–9) cm wide at base, the base often with a slight and corrugate neck, roughly striate with fine converging (sub-parallel) venation on both surfaces, glabrous or almost so on the outer surface, the inner surface with an abundance of appressed, bristle-like opaque hairs along the veins and a sparse cover of minute, dark brown, erect hairs between the veins, obscurely toothed on the lower margins. Auricles rudimentary and comprising a narrow tapered blade shoulder which is often corrugate; the lower margin of the blade, its shoulder and sometimes also the upper margin of the sheath with bristles to 10 mm long. (Fig. 5*b*,*c*).

Branching Branches absent from the lowest culm nodes to *c.* 0.5 m and usually from a 2–8 m section about and below the mid-culm; lower branches may be scattered or altogether lacking, or so regularly and sufficiently developed as to form a thicket around the clump base. Lower and upper branches morphologically well-differentiated but with some intergradation. Upper branch complements of 2–4 (–5) orders, of unrestricted monoclade form (*sensu* McClure 1973 per Wong 1995) (Fig. 5*e*) or trimerous around the mid-culm, not spinose; primary branches somewhat ascending or almost perpendicular to the culm, to 4 m in length. Basal branches of 2–3 (–5) orders, usually three per node, the central branch dominant and the lateral branches equal and almost perpendicular to it (Fig. 5*f*), but often reduced at the culm nodes and sometimes increased near the tips; inner part of the branch system rigid with the smaller branches forming thorns, the outer part flexuose and sparingly leafy, the leaves small; primary branch to 4 m in length, more or less perpendicular to the culm. Thorns slender, rigid, straight or slightly recurved, to 10 cm long, often multi-nodal and then bearing secondary thorns but rarely leafy shoots at the nodes (Fig. 5*g*).

Leaf Linear-lanceolate, or in larger leaves tending to lanceolate or narrowly elliptical, the base rounded, the tip acuminate (Fig. 5*a*), 5–20 by 0.8–3.0 cm, green, somewhat pubescent when young, the pubescence persisting sparsely on the undersurface, the central vein depressed above and raised below, central and secondary veins yellow or brown, secondary veins scarcely distinguishable from the tertiary above but quite distinct below, tertiary veins green, transverse veins not apparent. Pseudopetiole 2–4 by 1–2 mm, flattened dorso-ventrally, yellow, pubescent above and below. Sheath striate, yellow to yellow-green, finely fringed, finely pubescent when young with scattered hairs persisting mainly along the central vein; cupule prominent, with a raised rim; ligule often covered by chaffy scales dorsally, to 1 mm, or exceptionally to 3 mm long, with long cilia at times reduced to a short fringe or ragged edge; auricles on new growth comprising *c.* 5 filiform lobes to 2 mm, usually caducous.

Flowering pattern Gregarious, anecdotal records (unpubl. data) suggesting a flowering cycle of 41–51 years. Strictly semelparous (monocarpic), reproducing freely from seed.

Flowering branch To 2.5 m long and with up to 30 nodes, simple or sparingly branched at the lower nodes, sometimes complexly branched (Fig. 7*b*); arising by rapid unbranched apical extension of leafy branchlets and terminating in a pseudospikelet, but subsequently incorporating the original branchlet and often branching from the original growth (the *flowering long-shoots* of Wong 1995). Onset of flowering is accompanied by leaf loss; new growth of flowering branches support caducous leaf-like bracts (the inflorescence *sheath blades* of Wong 1995) to 8 by 1 cm but mostly less than 4.5 by 0.6 cm prior to development of the inflorescence (Fig. 7*j*).

Inflorescence (synflorescence) An irregular iterauctant cluster of 1–25 pseudospikelets. Pseudospikelets linear, slightly laterally compressed, to 45 (–70) mm long, comprising 2–4 glumes and up to 16 florets (Fig. 7*f*), the florets variously bisexual, male or sterile; fertile and especially bisexual florets mostly in the lower section of the spikelet; bisexual florets commonly more than one per spikelet. Pseudospikelet prophylls to 3 mm, lacking obvious keels or sometimes with a single, central keel, often oblique, the lateral wings fringed with cilia. Glumes boat-shaped, acute, glabrous or somewhat ciliate and with scattered pale hairs, unequal, the longest 4.5–8 mm in length and with *c.* 15 raised veins on the abaxial surface, the central vein (keel) slightly more prominent. Rachilla pubescent to densely hairy, flattened, jointed below the lemma; internodes 2–3 mm long, inflated below the joint.

Floret Bisexual, male and sterile florets similar externally or somewhat reduced above. Bisexual florets widely expanded at anthesis, exposing the stigmas and anthers at the same time. Lemma 7–9 mm long, acute to acuminate, similar in venation and texture to the empty glumes (Fig. 7*g*); palea of similar length to, or slightly exceeding the lemma, acute to acuminate, two-keeled and with strongly incurved margins, strongly ciliate on the upper portion of the keels, the inner surface glabrous (Fig. 7*h*,*i*). Ovary, stigmas and lodicules translucent white; ovary obovoid with scattered short cilia, *c.* 2 x 1 mm; stigmas 3, plumose, marginally exerted at maturity (Fig. 7*l*); stamens 6, the anthers 5 – 6 mm long, two-celled and emarginate, exerted on slender, free filaments to *c.* 10 mm long, the distal 15% of each cell opening at anthesis, lemon-yellow at anthesis, drying straw-coloured (Fig. 7*k*); lodicules usually 3, to 3 mm long, long-ciliate (Fig. 7*m*).

Seed A caryopsis shed individually with a section of rachilla attached, or as loosely-connected sections of the spikelet disarticulating above the glumes; 6.2–9.1 by 1.7–2.4 mm and 7.4 – 26.9 mg oven-dry (Table 1); ellipsoid; broader laterally than dorso-ventrally and broadest a little below the middle; grooved prominently on the ventral surface and finely on the dorsum; shortly, stoutly and bluntly beaked (Fig. 7*c*,*d*,*e*).

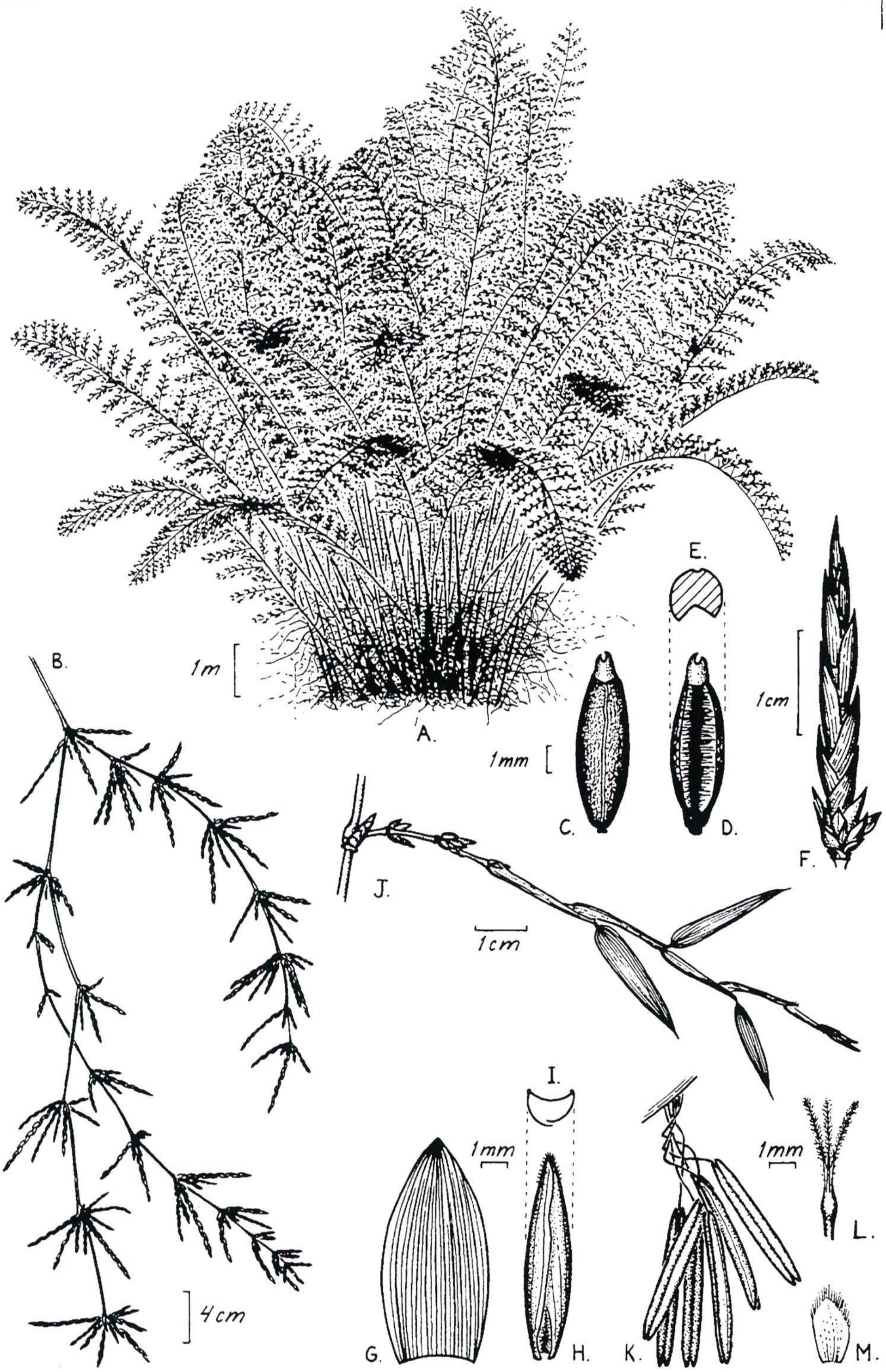


Figure 7. ***Bambusa arnhemica*****:** ***a.*** **leafy clump;** ***b.*** **flowering branch;** ***c., d., e.*** **seed;** ***f.*** **pseudospikelet;** ***g.*** **lemma;** ***h., i.*** **palea;** ***j.*** **developing flowering branch showing leaf-like inflorescence sheath blades;** ***k.*** **set of stamens;** ***l.*** **ovary and stigmas;** ***m.*** **lodicule.**

Illustration prepared by Monika Osterkamp Madsen. Some material has been reproduced or modified from Cowie *et al.* (2000) with permission.

Table 1. Weight and dimensions of seed of the bamboo *Bambusa arnhemica*.
n = 20.

Parameter	Mean ± s.d.	Range
Weight, air-dry	19.7 ± 4.98 mg	11.4 – 31.0 mg
Weight, oven-dry	17.2 ± 4.50 mg	7.4 – 26.9 mg
Length	7.6 ± 0.69 mm	6.2 – 9.1 mm
Width, dorso-ventral	1.7 ± 0.20 mm	1.3 – 2.0 mm
Width, lateral	2.1 ± 0.20 mm	1.7 – 2.4 mm

Seedling Initial culm 10–25 cm tall and 0.6–1.0 mm in diameter at the base, unbranched, with 6–10 leaves to 60 by 10 mm and 0–2 leafless nodes below.

Discussion

This description concords with but substantially extends those provided by Mueller (1886), Muller (1997) and Cowie *et al.* (2000). Features of the species include rudimentary (unlobed) culm sheath auricles, caducous leaf-like inflorescence sheaths, and the presence and arrangement of the thorns including their restriction to the basal branches. None of these features have previously been reported in the scientific literature (but see popular works by Brock 1993 and Muller 1997), herbarium material being confined to leaves and inflorescences. Mueller was apparently unfamiliar with the species in the field, his description being based on material sent by a local collector.

I can find no evidence to support suggestions (Mueller 1886, Bindon 1991, Spencer 1986, various current observers pers. comm.) that *B. arnhemica* comprises more than one taxon, or that a second species is present in the area, an opinion in concordance with that of Muller (1997). Morphological variation, particularly in the development of the basal branches and colour of the culm shoot, is considerable but gradational. One basis given for these suggestions is ecological: that whilst most *B. arnhemica* is riparian in occurrence, a small number of stands occur on rocky hillsides and coastal headlands. However, no absolute morphological variation is evident, though non-riparian *B. arnhemica* is shorter with smaller culm diameters, presumably reflecting harsher growing conditions. Furthermore, preliminary AFLP analysis of 27 polymorphic bands (Isagi, Tsukagoshi and Franklin unpubl. data) reveals no genetic dichotomy between riparian and non-riparian stands.

Approximately 140 species are attributed to *Bambusa* Schreb. (Ohrnberger 1999). Recent publications concerning its circumscription and relationships (Wong 1993*a*, Stapleton 1994, Widjaja 1997, Bedell 1997, Zhu Shilin *et al.* undated) emphasize a wide range of vegetative and floral traits with little agreement as to the definitive characters. Amongst Asian bamboos, thorny basal branches are unique to *Bambusa* (McClure 1966). Genetic analyses suggest that *Bambusa* is close to *Gigantochloa* and *Dendrocalamus* (Watanabe *et al.* 1994, Loh *et al.* 2000). Traits used to distinguish related genera are summarised in Table 2. Stapleton (1994) proposed, on the basis of Himalayan species, that *Bambusa* characteristically has two-keeled bud prophylla, a feature used to separate it from *Dendrocalamus*. *Bambusa arnhemica* does not have two-keeled bud prophylla, and use of the trait has not been taken up by subsequent workers.

By almost all criteria (Table 2), *B. arnhemica* is correctly placed in *Bambusa*. Furthermore, the development of the flowering branch as described here is identical to the detailed analysis provided for *Bambusa* by Wong (1995, pp. 120–127), including the presence of inflorescence sheath blades as illustrated by Wong for *B. farinacea*. However, *B. arnhemica* lacks the lobed culm sheath auricles that are generally a feature of the genus, a character reduction it shares with *B. balcooa* Roxburgh (Stapleton 1994).

At least 15 species of *Bambusa* are thorny (But *et al.* 1985, Benton and Weatherhead 1996, Ohrnberger 1999, this study). Whether thorniness has phylogenetic significance or is a labile and convergent trait with multiple origins within *Bambusa* is unknown. The origins of *B. arnhemica* are also unknown, and I have been unable to identify any potentially synonymous or closely related species. Muller (1997) suggested that *B. arnhemica* has affinities with the widespread and thorny *B. bambos* (L.) A. Voss (syn. *B. arundinacea*) and *B. blumeana* J. H. Schultes. *Bambusa arnhemica* differs from these species in its lack of lobed culm sheath auricles and in several other characteristics (Table 3). In *B. arnhemica*, basal branches, and thus thorniness, are more prominent in clumps whose lower culms are exposed to light (pers. obs.), and may even be quite absent. Hearne (1975) suggested that the thorniness of *B. arnhemica* could be minimised in

Table 2: Summary of traits used to distinguish *Bambusa* from related genera and successfully characterised for *B. arnhemica*.

Sources: Wong 1993*a*,*b*; Bedell 1997; Widjaja 1997; Zhu Shilin *et al.* undated.

Trait	Genus and characteristics
Nodes	*Bambusa* - collar slightly raised *Fimbribambusa* - spreading "crest" on each node
Culm internodes	*Neololeba* - longer below branches than above *Bambusa* - not different below and above branches
Branch complements	*Bambusa* - derived from a single bud, one branch dominant *Kinabaluchloa* - all branches sub-equal *Holttumochloa* - derived from many primary buds
Basal branching	*Bambusa* - present *Dendrocalamus*, *Gigantochloa* & *Neololeba* - absent
Bud prophylls	*Bambusa* - not divided *Holttumochloa* - divided into very unequal lobes
Leaves	*Bambusa* - small, lacking obvious transverse venation *Dendrocalamus* - large, with usually obvious transverse venation *Gigantochloa* - large
Culm sheath base	*Bambusa* - smooth; *Soejatmia* - wrinkled
Flowering branches	*Bambusa* - rebranching during flowering *Holttumochloa* - remaining unbranched
Inflorescence	*Bambusa* - clustered *Dendrocalamus* & *Gigantochloa* - large, compound
Pseudospikelets	*Bambusa* - linear, many-flowered, with 3 or more perfect flowers *Maclurochloa* - containing only 1 or 2 perfect flowers
Subtending bracts	*Bambusa* - bract distinctly smaller than the lemma on higher than first-order pseudospikelets *Kinabaluchloa* - bract almost as long as the lemma on higher than first-order pseudospikelets
Rachilla internodes	*Bambusa* - elongated, disarticulating below the lemma *Dendrocalamus* & *Gigantochloa* - short, not disarticulating *Neololeba* - short
Glume hairs	*Bambusa* - pale; *Gigantochloa* - dark
Palea	*Bambusa* - rounded, truncate or slightly cleft at the summit *Soejatmia* - apex distinctly bifid
Ovary	*Bambusa* - obovoid-ovoid when young, ciliate *Kinabaluchloa* - slender-cylindric and tapering upwards when young; *Neololeba* - elongated; *Fimbribambusa* - glabrous
Stigmas	*Bambusa* - 3; *Dendrocalamus* - 1, sometimes bifid or trifid at tip
Filaments	*Bambusa* - free; *Gigantochloa* - fused into a tube
Lodicules	*Bambusa* - 3; *Dendrocalamus* - none, or sometimes 1 or 2; *Neololeba* - none
Caryopsis	*Bambusa* - ovoid; *Gigantochloa* - narrowly cylindric

Table 3: Traits of the two widespread Asian thorny bamboos that serve to distinguish *Bambusa arnhemica* .

Sources: Dransfield & Widjaja (1995), personal observation. For a comparison of *B. arnhemica* with the two other Australian woody bamboos, see Chapter 7.

Taxon	Distinguishing traits
Bambusa bambos	- culms to 30 m x 15-18 cm
	- branched at all nodes
	- thorns robust, often occurring on upper branches and giving rise to leafy shoots
	- culm sheath auricles forming a prominent wrinkled margin
	- culm blade broadly triangular
	- leaves slightly glaucous beneath
	- pseudospikelets *c.* 2 cm long
Bambusa blumeana	- culms to 20 cm diameter
	- upper branches branched at base
	- hairs on back of culm sheath (if present) dark brown
	- lower culm sheaths short and narrow
	- culm sheath auricles to 5 mm long
	- culm blade to 15 x 1.5 cm, with dark hairs
	- thorns robust, often occurring on upper branches and giving rise to leafy shoots

cultivation by watering and application of fertiliser. There are three native species of "woody" bamboo in mainland Australia (Spencer 1986, Muller 1997, Mallett and Orchard 2002), of which only *B. arnhemica* is thorny. Although all have been placed in *Bambusa* (but see Widjaja 1997), they are quite dissimilar (Muller 1997). This suggests that bamboo may have colonised Australia from the north on at least three occasions.

Liddle *et al.* (1994) and Mallett and Orchard (2002) reported outlying occurrences of *B. arnhemica* at Cobourg Peninsula (11°22'S, 132°09'E) and South Goulbourn Island (11°40'S, 133°23'E) (Fig. 1). Examination of leaf material from both locations, and of a photograph of a culm shoot from Cobourg Peninsula, clearly identifies these records as erroneous and possibly referrable to a green form of *B. vulgaris* Schrader ex Wendland.

Leaf material differs from *B. arnhemica* in having (on smaller branches, at least) a raised, 1 mm wide sheath scar forming a distinct lip perpendicular to the culm surface, a prominent supra-nodal ridge, and robust and apparently non-deciduous leaf auricles. The Cobourg Peninsula occurrence is restricted to the immediate vicinity of an historic garden (Alan Withers, pers. comm.) to which plants were introduced from the Sydney Botanic Gardens and Timor (Spillett 1979). It seems likely that both occurrences are the result of deliberate introductions, and it is unclear whether they can even be regarded as naturalised. Material from Melville Island (11°50'S, 130°50'E, Fig. 1), where extensive wild stands of bamboo are to be found near the south coast, is confirmed as *B. arnhemica*.

Other than *bamboo*, there is no well-established vernacular for *B. arnhemica*. It has been termed *Native Bamboo* and *Arnhemland Bamboo* (Spencer 1986, Clarke and Traynor 1987). The former is unhelpful nationally or internationally, and on current definitions of Arnhemland, the latter is inappropriate. *Top End Bamboo* is recommended as distinctive and appropriate.

Acknowledgements

The Ostwald and Briggs families kindly permitted me to work on their properties at Mary River Park and Mt Bundy Station respectively. For their comments on taxonomic methods and implications, I am grateful to Len Muller, Ian Cowie and Soejatmi Dransfield. Mark Traynor, Chris Mangion and Jenny Risler helped track down the Cobourg Peninsula bamboo record. David Bowman, Phil Short, Peter Whitehead and Len Muller commented helpfully on an earlier draft. Monika Osterkamp Madsen prepared the botanical illustrations, and Daniel McIntyre prepared the map. This work was supported by the Parks & Wildlife Service (Northern Territory) and the Key Centre for Tropical Wildlife Management at Northern Territory University.

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Chapter 3:

Landscape and vegetation

This chapter has been submitted as:

Franklin DC, Bowman DJMS. A multi-scale biogeographic analysis of *Bambusa arnhemica*, a bamboo from monsoonal northern Australia.

Abstract

Aims

To identify the edaphic, environmental and historical factors influencing the patchy distribution of the semelparous bamboo *Bambusa arnhemica* F. Muell. at global, catchment and streambank scales.

Location

The entire range of *Bambusa arnhemica*, a highly fire-prone savanna matrix with generally infertile soils in the north-west of the Northern Territory of Australia above the 1,200 mm mean annual rainfall isohyet.

Methods

Distribution surveys were conducted by air, boat and on the ground. Plot data were collected throughout the entire range of the species.

Results

Bambusa arnhemica occurred predominantly on floodprone but nevertheless well-drained and deep alluvial soils mostly on sloping stream banks, but ranged widely along lentic watercourses from ephemeral headwater streams to the banks of major rivers and levees on the coastal floodplain. Savannas immediately adjacent to *B. arnhemica* gallery forests were also floodprone and on deep alluvial soils, but were upslope on level ground. Its infrequent non-riparian occurrences were on a wide variety of substrates but generally on soils of moderate fertility and in coastal and/or rocky areas where at least partial topographic protection from fire is likely. Within and between catchments, the distribution of *B. arnhemica* was idiosyncratic, occurrence being almost always continuous downstream from highly variable "starting" points to the poorly-drained coastal floodplain.

Main conclusions

At local scales, *B. arnhemica* appears constrained by poor drainage and high fire-frequencies. Enhanced soil fertility may increase its capacity to cope with fire. At the catchment and global scales, we propose that the distribution of *B. arnhemica* is the product of infrequent and as yet incomplete dispersal across and away from watercourses by seed that lacks specialised dispersal mechanisms, combined with passive dispersal along streams. From this we infer that *B. arnhemica* is neither a very recent, nor very ancient colonist from Asia. *Bambusa arnhemica*'s circumscribed global distribution has no parallel amongst co-occurring rain forest plants and may be the product of poor dispersal capacity and a substantial rock and floodplain barrier to the east. Limited dispersal capacity may be inextricably linked to local domination of space and the subsequent creation of regeneration space by parental death.

Introduction

Canopy or understorey monodominance by woody bamboos (Poaceae: Bambuseae) presents an interesting ecological counterpoint to the species-rich forests and woodlands of both the old and new world biological realms. Dominance by woody bamboos has been documented in Amazonian lowland rain forests (Nelson, 1994; Silveira, 1999), central American highland forests (Widmer, 1994), South American temperate rain forests (Veblen, 1982; Pearson *et al.*, 1994), Asian temperate and highland sub-tropical forests (Numata, 1979; Taylor *et al.*, 1996), Asian deciduous tropical forests and savannas (Singh *et al.*, 1985; Marod *et al.*, 1999), and in riparian and vine-thicket vegetation embedded within tropical wooded savannas in northern Australia (Franklin & Bowman, 2003). The vigorous, clonal growth form of woody bamboos may facilitate this dominance (Okutomi *et al.*, 1996), suppressing regeneration by co-existing trees. However, the unusual life history of many bamboos, in which considerable longevity is combined with gregarious flowering and subsequent die-off (Janzen, 1976; Keeley & Bond, 1999; Franklin, in press) may provide infrequent periodic release from competition for co-existing species (Taylor & Qin Zisheng, 1992; Gratzer *et al.*, 1999; Narukawa & Yamamoto, 2002; Gonzalez *et al.*, 2002; Griscom & Ashton, 2003).

Despite the competitive success of the bamboo lifeform and reproductive strategy, its dominance is characteristically restricted to localized patches within the broader landscape (e.g. Numata, 1979), raising questions about the cause and stability of patch boundaries. Gregarious occupation of space may be a feature of bamboo life histories (Keeley & Bond, 1999; Franklin & Bowman, 2003). Nelson (1994) documented an extreme example of patchiness, in which 92,000 km^2 of bamboo-dominated forest in Brazilian Amazonia had margins that were "circular or amoeboid in shape". Dynamic interactions between bamboo and forest trees at these boundaries (Silveira, 1999; Griscom & Ashton, 2003) have prompted the suggestion that these shapes are the product of recent invasion (Judziewicz *et al.*, 1999). There are few studies, however, that attempt to identify the environmental conditions that constrain or favour natural bamboo stands, and even fewer that quantify distributions at landscape scales.

However, an oft-repeated theme is that interactions between bamboo and forest trees may be moderated by natural or anthropogenic disturbance including clearing and fire. Bamboo dominance is often promoted by disturbance (Wong, 1991; Silveira, 1999; Banana & Tweheyo, 2001), but such effects are not unqualified. Reid *et al.* (1991) found that a Chinese sub-alpine understorey bamboo grew best at mid-altitudes and in filtered light conditions, but that disturbance in the form of clear-felling of associated trees promoted dominance by short, thin-culmed stands of bamboo. Stern *et al.* (1999) noted that, whilst an understorey bamboo often dominated forest clearings, seedlings only survived within the forest, suggesting that dominance arose vegetatively as a short-term response to disturbance.

In a previous study, we presented evidence that, whilst seedlings of the semelparous north Australian bamboo *Bambusa arnhemica* F. Muell. were resilient to disturbance by fire and flood, there were no indications that disturbance other than parental death promote regeneration (Franklin & Bowman, 2003). Based on an intensive study of contrasting alluvial riparian and rocky hillside sites, we suggested that the species was restricted to *relatively* fire-sheltered topographic locations embedded within a fire-prone tropical savanna, a situation that parallels the occurrence of rain forest and vine-thicket in the region (Russell-Smith, 1991; Bowman, 1992).

Bambusa arnhemica is an ideal species to address the issue of the environmental controls of monodominant bamboo at both the patch and landscape scale because of the absence of large-scale land clearing throughout the species range. In this study, we examine the generality of our previous observations about the position of *B. arnhemica* in the landscape. We consider its distribution at three spatial scales: *a.* the broad geographic limits of its occurrence; *b.* longitudinal occupation of river systems; and *c.* lateral (streambank) occupation of gallery forests and other riparian vegetation. Taking advantage of the linear nature of most of the habitats in which it occurs, its local abundance but fairly restricted range (*c.* 300 x 250 km, Franklin, 2003*a*), and its ready detectability from the air, we present a high-resolution view of its entire range and an interpretation of the factors influencing it. This is complemented by plot-based studies of *B. arnhemica* stands and adjacent vegetation sampled throughout the range of the species. In so doing, we address two questions from a geographic perspective: (1) what edaphic constraints limit *B. arnhemica*? and (2) to what extent are the local and global limits to the distribution of *B. arnhemica* imposed by ecological processes such as high fire frequencies and limited dispersal capability?

Methods

The species

Bambusa arnhemica is a pachymorph (clumping) bamboo with 10–20 m tall culms that often occurs in monodominant stands. It is long-lived and gregariously semelparous, both above- and below-ground parts dying after flowering. Death is accompanied by prolific regeneration from seed. The seed is a large caryopsis (mean air-dry weight 19.3 mg) with no apparent adaptations to enhance dispersal. For background information on the species, refer to Franklin (2003*a,* in press) and Franklin & Bowman (2003).

The species is endemic to the north-western Top End of the Northern Territory of Australia (Liddle *et al.*, 1994). It is the sole woody bamboo in the Northern Territory and one of only three in mainland Australia, the dissimilarity of which (Muller, 1997) suggests that bamboo has colonised Australia from Asia on at least three occasions (Franklin, 2003*b*).

Distribution survey

The interim distributional limits of *B. arnhemica* (Liddle *et al.*, 1994) were identified from the records of the extensive rain forest survey of Russell-Smith (1991), collections and field data of the Darwin Herbarium, and field data from the Bioregional Assessment Unit of the Department of Infrastructure, Planning & Environment. Two outlying records (shown in Liddle *et al.*, 1994) were investigated and found to be misidentifications (Franklin, 2003*a*). Apparent boundaries were then "pushed" by seeking advice from numerous informants with knowledge of key areas, but found to be broadly robust. Information was also sought from informants about occurrence on specific watercourses within the known range, and of non-riparian occurrences.

Within the general distribution of the species (Fig. 1), all major and many minor watercourses were surveyed mostly by air and sometimes by boat or from the ground. Air surveys were conducted during the wet seasons of 2000/01 to 2002/03 from a single-engined fixed-wing-above aircraft flying at 150 km/h and 150 m above the ground. A GPS operator recorded a waypoint every 30 seconds, corresponding to a 1.3 km segment of riparian vegetation, and conveyed the waypoint number to the observer (always DCF). For each segment, the observer made a qualitative assessment of the relative abundance of *B. arnhemica* on a scale of 0–10 where zero means none observed, three corresponds to the presence of at least 10 clumps, and ten to a ± continuous canopy on at least one bank. In boat and linear land-based surveys, presence/absence was recorded for 1 km segments. Presence/absence was also recorded by point-based observation at intersections of roads and streams. Along the Adelaide River downstream from the Arnhem Highway crossing, a region where *B. arnhemica* occurred only sparsely, the location of each patch was recorded.

Non-riparian records of *B. arnhemica* were obtained from the author's incidental observations, by air survey of the Daly Range, Mt Bundey Hills and hills on Annaburroo Station, and by following up reports from other observers.

Surveys were influenced by the occurrence of mass-flowering and die-off, which commenced in *c.* 1996 and become extensive during and after 1998, affecting an estimated 15% of stands prior to the 2000/01 survey. Dead clumps remain standing for two to five years. During the wet season, clumps that are flowering or have died but remain standing are more obvious from the air than mature leafy clumps. Most areas were surveyed either prior to or during mass-flowering or in the period when dead culms remained standing. Of the exceptions, the area close to Darwin was surveyed from the ground, leaving only the upper parts of the McKinlay River and Goodparla Creek (estimated at about 1% of all stands) as somewhat ambiguous.

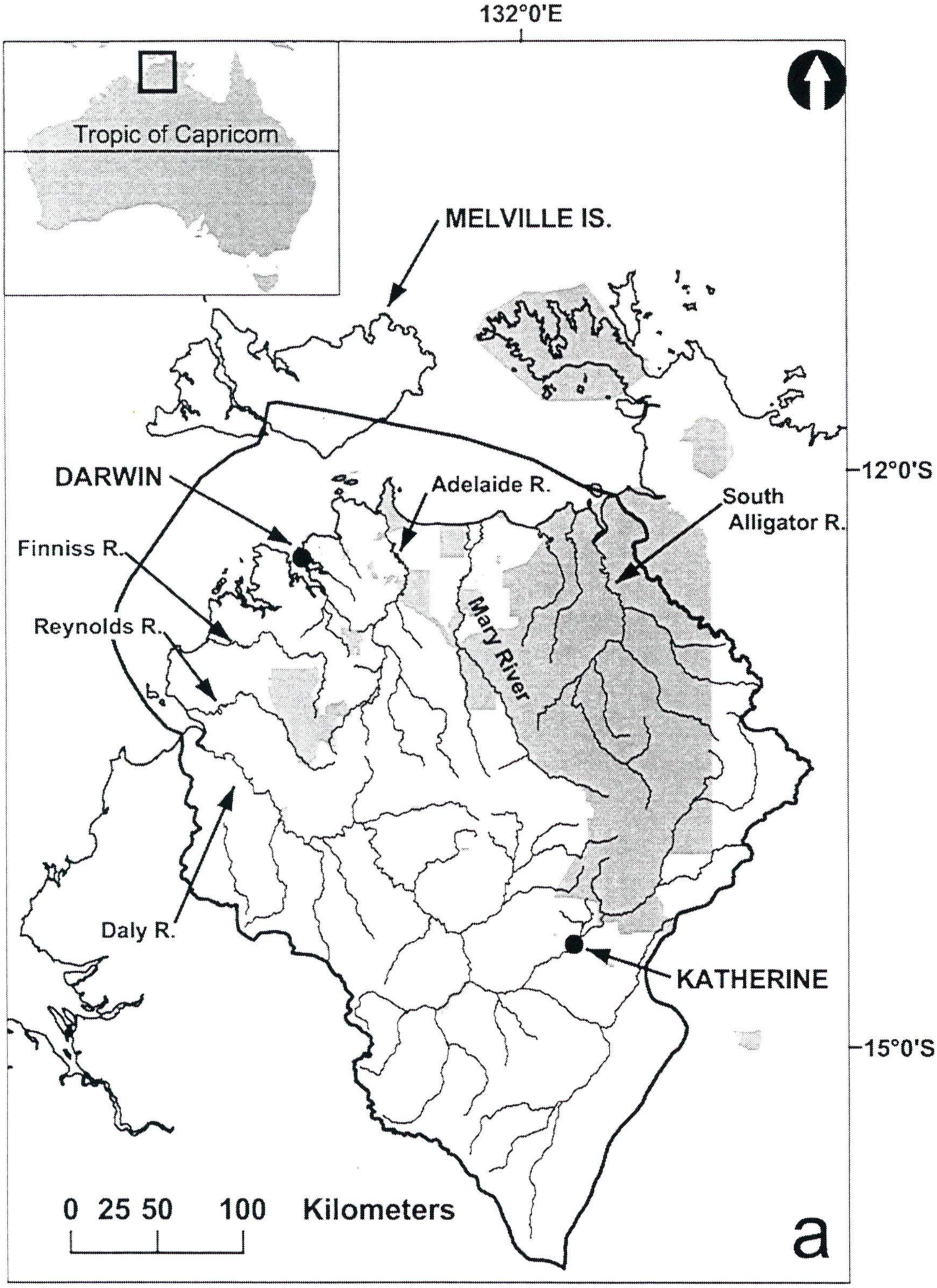
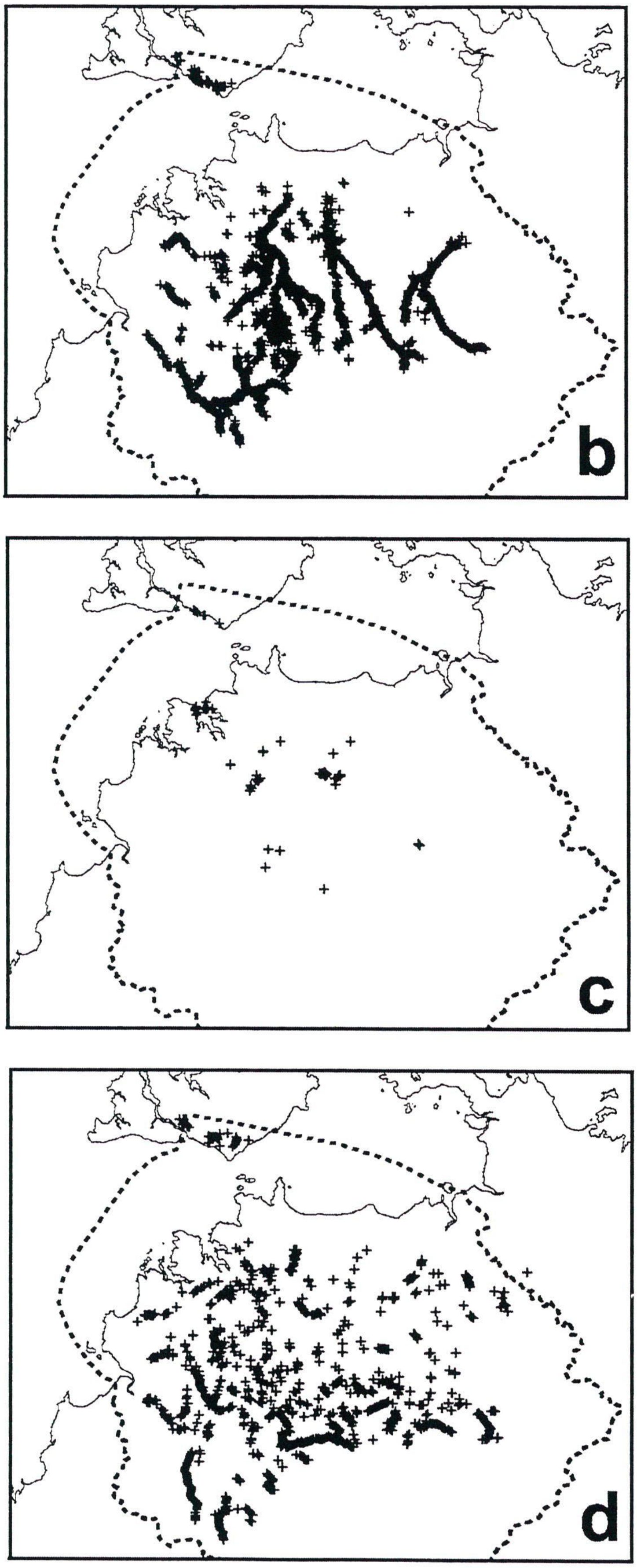


Figure 1: *a.* Study area, showing main watercourses, with a frame around the combined catchments in which *Bambusa arnhemica* F. Muell. occurs; *b.* (next page) riparian records of *B. arnhemica* (n = 1,640); *c.* non-riparian records of *B. arnhemica* (n = 58); & *d.* riparian locations surveyed at which *B. arnhemica* was not detected (n = 916).

Grey areas in the main map are conservation reserves.



Figs. 1*b*, *c* & *d*. Caption on previous page.

Plot data

Plot-based studies were conducted at 35 riparian and six non-riparian *B. arnhemica* sites widely dispersed throughout the range of the species (Fig. 2). Sites were selected to represent the range of situations in which the species occurs, and were 5–10+ km apart except where the environmental setting contrasted sharply. Sites were assessed during the dry seasons of 2002 and 2003.

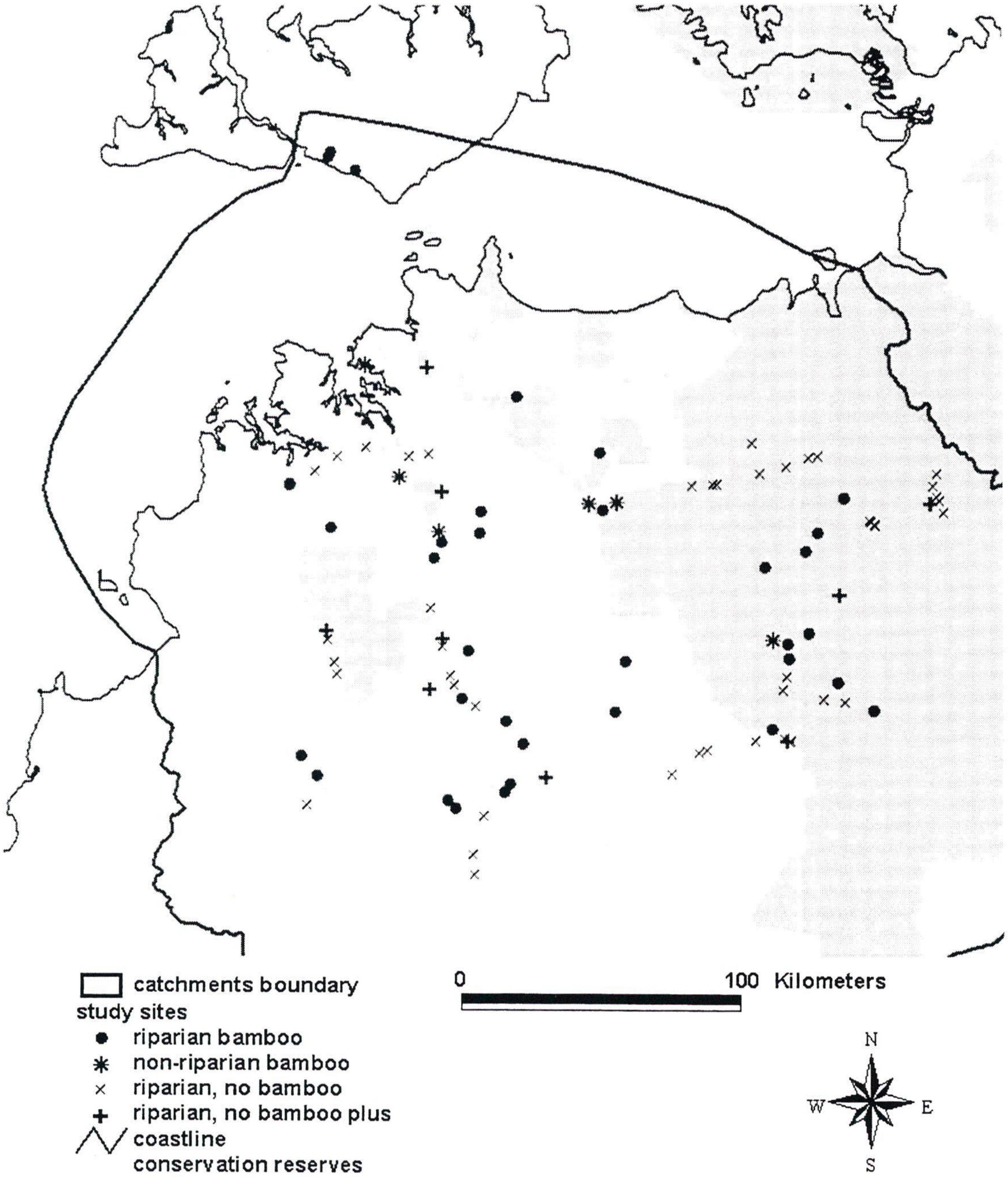


Figure 2: Location of 35 riparian and 6 non-riparian *Bambusa arnhemica* F. Muell. plots, and of 54 "no bamboo" riparian assessments sites including 9 ("plus") for which the depth of riparian vegetation was assessed (see Methods).

At each site, a study plot was established within the vegetation that contained *B. arnhemica* and positioned to include at least five *B. arnhemica* clumps. In defining areas suitable for sampling with these plots, outlying clumps of *B. arnhemica* were ignored (and thus show up occasionally in adjacent "non-bamboo" plots). At riparian sites, a second plot was established in the non-bamboo vegetation adjacent but away from the watercourse, and where woody vegetation occurred downslope between the *B. arnhemica* vegetation and the watercourse, a third plot was established there. All plots were 100 x 20 m subject to site constraints. At riparian sites, plots were invariably 100 m long and generally parallel to the watercourse, width being constrained quite frequently by the width of the relevant vegetation band. Where the riparian band containing *B. arnhemica* was more than 20 m wide, the long side of the plot was angled across the slope to embrace the range of variation associated with the slope.

In each plot, the following were assessed: location, slope, aspect, parent material, soil texture, surface rock cover, litter cover, vegetation structure, cover of life forms, evidence of fire and evidence of moisture seepages. Location was recorded with a GPS, slope and canopy height measured with a clinometer, and aspect with a compass. Soil texture was assessed using the squeeze test of McDonald *et al.* (1990) on one to three surface samples moistened to field saturation, and classified as sand, sandy loam, loam / silty loam, clay loam or clay. Surface rock cover was assessed at 100 points at 1 m intervals along the central axis of the plot as soil, or as rock in diameter classes of <1, 1–5, 5–10, 10–50, 50–100, >100 cm. Vegetation structure was recorded as height and cover (modified Braun-Blanquet scale: 1 = <1%,2 = 1–5%, 3 = 5–10%, 4 = 10–25%, 5 = 25–50%, 6 = 50–75%, 7 = 75–100%) of the canopy, shrub and forb layer. Litter and life form cover was also recorded using the modified Braun-Blanquet scale, the latter for each of: bamboo, trees - eucalypts (*Eucalyptus* and *Corymbia*), trees - *Melaleuca*, trees - *Acacia*, trees - *Erythrophleum*, trees - *Lophostemon*, palms, other rain forest trees with notophyll or smaller leaves, other rain forest trees with mesophyll or larger leaves, pandani, other woodland trees, woody vines, herbaceous creepers, cycads, rain forest shrubs, woodland shrubs, grasses (excluding *B. arnhemica*), ferns, other forbs. Trees were defined as being taller than 5 m. Plants were classified as rain forest species generally following Liddle *et al.* (1994). .

In *B. arnhemica* plots, additional data collected were: the identity and cover (modified Braun-Blanquet as above) of all plant species with more than 1% cover along with those with less than 1% cover where readily recognised; and whether mass-flowering had occurred in recent years. At riparian sites, additional data collected were: the depth of the riparian vegetation, measured step-wise with a clinometer; whether the adjacent stream was tidal and/or had permanent water and if not, an estimate of the annual period of flow; the width of the gallery vegetation on one bank, in classes of < 5, 5–10, 10 –20, 20 –50, 50 – 100 and > 100 m; and the horizontal proportion of the riparian vegetation occupied by *B. arnhemica*, in classes of <20, 20 – 50, 50 – < 100, 100 and > 100 % and whether this was in the lower, middle or upper portion of the riparian vegetation. In plots adjacent to *B. arnhemica* stands, a floristic descriptions of dominants was made.

Assessment of absence

Upon completion of the plot survey of *B. arnhemica* sites, a *post hoc* qualitative survey of riparian sites lacking *B. arnhemica* was undertaken throughout the range of *B. arnhemica* but excluding the coastal plain (Fig. 2). These non-bamboo sites were classified as falling outside the environmental envelope of *B. arnhemica* if they fitted any of the following criteria: *a.* the substrate for riparian vegetation was rocky; *b.* the riparian vegetation was dominated by *Melaleuca* throughout or *Melaleuca* with an upslope fringe of *Lophostemon lactifluus* (F.Muell.) Peter Wilson & J.T.Waterh.; *c.* there was evidence other than *b.* that the entire riparian strip was poorly-drained; or *d.* there was no riparian vegetation, the savanna extending to the downslope edge of woody vegetation. In the course of this *post-hoc* survey, the stream bank depth of riparian vegetation was assessed (method as previous) at those sites that fitted criterion *b* above *and* backed directly on to eucalypt savanna.

To determine if rock cover was consistently associated with the absence of *B. arnhemica*, the following survey was conducted at Middle Creek in the Daly River catchment (13°49'S, 131°20'E), a site selected because *B. arnhemica* and emergent bedrock occurred interspersed along the watercourse. The cover of *B. arnhemica* seedlings, woody vegetation and rock were assessed using the modified Braun-Blanquet cover scale in 10 m bands of riparian vegetation perpendicular to the watercourse at 50 m intervals along the watercourse as determined with a GPS.

Analysis

For each site in the distribution survey, the coordinates along with an estimate of altitude determined from a Digital Elevation Model were input into the BIOCLIM module of the climatic modelling program ANUCLIM (Houlder *et al.*, 2003) to yield a summary of rainfall and temperature parameters. However, as the estimates of mean annual rainfall were demonstrably substantially inaccurate when matched against the few available rainfall stations in the region, mean annual rainfall estimates included here are derived by interpolation from contour maps available at the Commonwealth Bureau of Meteorology web-site, *www.bom.gov.au.*

For plots and select other sites, altitude was determined more accurately from 1:100 000 or finer-scale topographic maps. Parent materials were determined from 1:100 000 and 1:250 000 geological maps and some rock samples, both interpreted in consultation with a professional geologist. Catchment and sub-catchment areas were calculated in ArcView GIS 3.2 (ESRI 1992–2000) using a Digital Elevation Model with 274 m cells and the D8 flow direction algorithm. For the purpose of this study, a "sub-catchment" is the catchment area of a given site.

The five soil texture classes were allocated numbers from one to five on a gradient from coarse (sand) to fine (clay). Where there was variation within plots, the plot was attributed to the predominant soil type or to the mean value for soil types present.

Most statistical analyses were conducted in Statistica (StatSoft Inc., 1984–2002). Classification, ordination, *post-hoc* Multi-response Permutation Procedures (MRPP) and *post-hoc* vector-fitting (joint plots) were conducted using PC-Ord (McCune and Mefford, 1999), in all cases using the Bray-Curtis distance measure. Ordinations were Non-metric Multidimensional Scaling with a maximum of three dimensions, conducted on cover scores for either plant species or life forms. *Post-hoc* vector fitting was conduced separately with the dependant variables (i.e. those used to produce the ordination) and independent site attributes. For the ordination of *B. arnhemica* plots alone, the site attributes were: altitude, soil texture, rock cover, slope and $\log_{10}$(catchment area), the latter being scored as zero for non-riparian sites. For the ordination of riparian *B. arnhemica* plots and adjacent plots, the site attributes available independently for each plot were slope and soil texture.

Exploratory multiple analyses of a single data set were conducted with a Bonferroni correction to α; reported probabilities are the corrected values; for example, $P = 0.05$ indicates that the test results corresponded to a probability of $0.05/n$ where n is the number of tests conducted on the dataset; application of the Bonferroni correction is always and only as stated. Results were considered significant at $P < 0.05$.

Results

Global distribution

Bambusa arnhemica was recorded from 1640 riparian locations or segments (Fig. 1*b*) and 58 non-riparian locations (Fig. 1*c*). All records were within 160 km of the coast in the north-west of the Northern Territory, Australia between latitudes 11 and 14°30' and longitudes 130 and 133°. This distribution embraces six adjacent major (2,000 – 55,000 km^2) and several minor mainland catchments, and a limited area of small catchments (max. 247 km^2) within 7 km the south-west coast of Melville Island. Examination of Herbarium and other flora survey records and consultation with field workers with appropriate relevant experience provided no evidence of occurrence beyond this general outline, specifically including catchments immediately to the east and south, the Daly River upstream of locations recorded in this survey, or other portions of Melville Island. Within or close to the recorded range of *B. arnhemica*, apparent absence was noted at 916 riparian locations or segments (Fig. 1*d*).

Reflecting the low-lying nature of the region, records were from sea-level to 240 m altitude. The mean annual rainfall at all *B. arnhemica* locations exceeded *c.* 1200 mm, but was intensely seasonal with median rainfalls for the driest quarter (approximately June – August) being zero throughout its range (Table 1). The generalised soil Moisture Index exhibited seasonal extremes paralleling rainfall, though this does not take into account local factors such as soil depth or supplementary moisture sources. Mean temperatures were high throughout the year at all sites, there was relatively little diurnal variation in temperature, and minimum temperatures (averaged for the coldest week across years) exceeded 12°C.

Table 1: Climatic summary of *Bambusa arnhemica* F. Muell. sites.

All climatic parameters except Mean annual rainfall have been calculated for 1698 *B. arnhemica* sites. Quarters are 3-month periods, estimated to the nearest week. Both quarters and weeks were determined from averages across years. See *Methods - Analysis* for more detail.

Parameter	Mean ± s.d.	Min.	Max.
Mean annual rainfall (mm)		1200	1750
Rainfall seasonality (1)	∞	∞	∞
Mean Moisture Index of highest quarter (2)	1.00 ± 0.00	0.99	1.00
Mean Moisture Index of lowest quarter (2)	0.01 ± 0.00	0.00	0.02
Mean temperature (°C)	26.7 ± 0.23	25.4	27.5
Mean temperature of warmest quarter (°C)	29.1 ± 0.31	28.0	29.9
Mean temperature of coldest quarter (°C)	23.3 ± 0.52	21.8	25.1
Mean diurnal temperature range (°C)	12.5 ± 1.08	8.9	13.9
Maximum temperature of warmest week (°C)	36.0 ± 0.92	33.2	37.4
Minimum temperature of coldest week (°C)	14.5 ± 1.19	12.7	18.8

(1) Calculated as the ratio of the median rainfall for the wettest quarter of the year over the median rainfall for the driest quarter of the year.

(2) The Moisture Index is a measure of soil moisture, ranging from 0 (dry) to 1.0 (saturated). See Houlder *et al.* (2003) for details.

Regional patterns from distribution data

In four of the six major mainland catchments, *B. arnhemica* was widespread (Fig. 1*b*) and often abundant (e.g. Fig. 3) along the main and some tributary streams. It ranged from minor watercourses in hill country at 40–165 m altitude to, but only sparingly on, the broad coastal floodplains at sea-level, where it was mostly associated with levees. On the Reynolds River, the distribution was broken by 30 km gap. On the Daly River, *B. arnhemica* was recorded only in the lower catchment although on downstream tributaries to near their headwaters at 130 m (see Franklin in press for more detail of the distribution of *B. arnhemica* in the Daly River catchment). On all systems, its occurrence at the scale of 1.3 km segments was decidedly non-random, occurrences generally taking the form of ± continuous stands below a well-defined upstream limit. Upstream limits varied greatly within and between catchments, with "bamboo-free" sub-catchments ranging from less than 1 km^2 to more than 40,000 km^2. In a number of cases, *B. arnhemica* was abundant along a major watercourse but extended only slightly or not at all up tributaries, for example, in the upper Mary River area (Fig. 3).

Occupied watercourses ranged from primary to sixth-order, and from large, perennial rivers and stranded meanders with permanent pools, through small spring-fed streams to intermittent minor streams that flow only during the wet season and lack persistent pools or any evidence of ground water. All watercourses were of low gradient (estimated $<< 1°$), and so far as could be determined from geological maps, their banks universally comprised Quaternary alluvial sediments. The background material from which these alluvial soils are presumed to have derived varied greatly, including unmodified sandstones and other sedimentaries (mainly the South Alligator River), limestone (Daly River) and a wide-range of metasedimentary parent materials. Several ephemeral streams incised deeply into a Kaolinised escarpment on Melville Island, the gradient of an intermediate portion of one of which was measured at 2°, provided exceptions to the above generalities.

The 58 non-riparian stands were widely dispersed through the species' range and from sea-level to 240 m altitude (95% at < 150 m), but often occurred in discrete clusters (Fig. 1*c*) associated with geological features (Table 2). Coastal stands (17) were on both lateritic (n = 10) and sandy (n = 7) substrates around Darwin Harbour and the south coast of Melville Island. Inland stands (41) were mostly (93%) on rock outcrops and often on the leeward side (W-N-W) of prevailing dry season winds, with a diversity of parent materials involved. Non-riparian stands were invariably small, two comprising a single clump and only two estimated to exceed 2 ha in area.

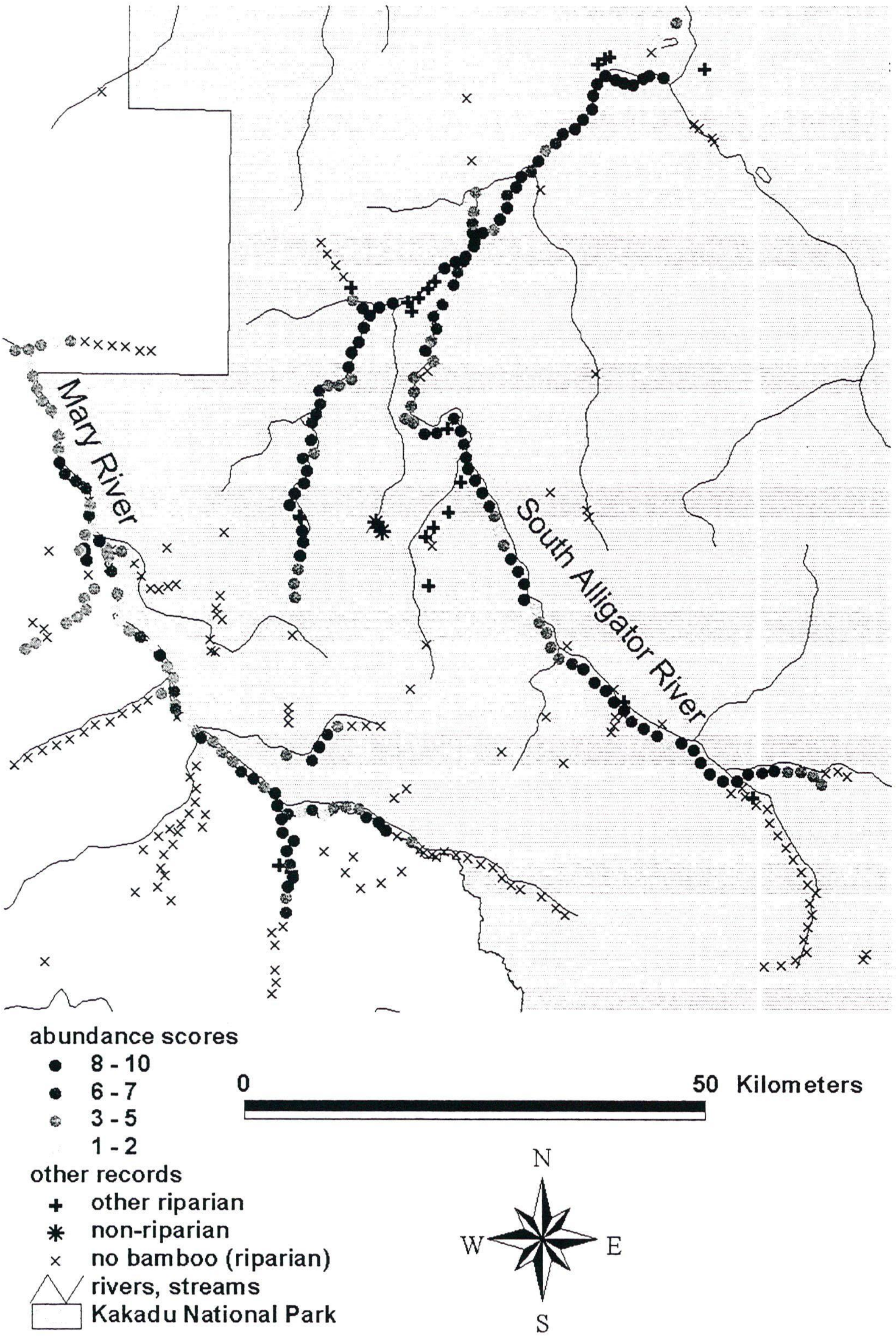


Figure 3: Abundance and distribution of *Bambusa arnhemica* F. Muell. in Kakadu National Park and adjacent areas.

Abundance scores are for 1.3 km segments of watercourse, determined from air surveys (see *Methods*), a score of 10 corresponding to a ± continuous canopy along at least one bank of the watercourse, and a score of 3 to a minimum of 10 clumps.

Table 2: Parent material of 58 non-riparian bamboo *Bambusa arnhemica* F. Muell. stands.

Age	Parent material	No. of sites	Notes
Quaternary	marine deposits	1	small coastal stand, Darwin
Quaternary	alluvial deposits	1	few clumps on edge of rain forest
Quaternary	*in situ* sandy soil	5	all on Melville Island coast; sands overlying sandstone
Cenozoic / Cretaceous	Cretaceous sedimentaries and their derived Cenozoic laterites	13	11 Darwin sites, all coastal or nearby; at base of coastal cliffs and other talus screes, on lateritic plateaus, and residual islands.
Early Proterozoic	metasedimentaries* – arenites (sandstone & quartzite)	19	14 sites on Daly Range & Acacia Ridge; all on resistant, ridge-forming rocks; see Franklin & Bowman (in press) for detail of one Daly Range site
Early Proterozoic	metasedimentaries* – ferruginous siltstone	3	dispersed; one extensive and two very small stands
Early Proterozoic	metasedimentaries* – pelites (siliceous siltstones)	5	Annaburroo Station; interspersed geology leaves doubt about some
Early Proterozoic	igneous - granite	*c.*11	all in Mt. Bundey Hills

* *metasedimentaries* – non-crystalline, low-grade metamorphic rocks with sedimentary characteristics fully preserved

Regional environmental attributes from plot data

Riparian *Bambusa arnhemica* almost invariably occurred on incised stream banks (both depositional and erosive) or low-profile levees on the coastal floodplains, one site being an overflow floodplain. There was much variation in the profile of streams on which it occurred and in the slope and soil characteristics within *B. arnhemica* plots (Fig. 4). Bank depth, riparian strip width and sub-catchment area were all positively correlated (Table 3) notwithstanding a tendency for bank height to decline and watercourses to form anabranch systems as they entered the coastal plain. The horizontal proportion of the riparian strip occupied by *Bambusa arnhemica* was negatively correlated with strip width and sub-catchment area, *B. arnhemica* tending to occupy the full width of riparian vegetation only on watercourses with a sub-catchment area of less than 1,000 km^2 (Fig. 5).

Riparian *B. arnhemica* plots were on deep alluvial soils with one possible exception on Melville Island, but the texture of these varied greatly (Fig. 4*f*). However, *B. arnhemica* rarely grew on unconsolidated sand and then only when there was a well-consolidated *B*-horizon close to the surface. There was no significant relationship between either soil type or bank slope and other physical site parameters (Table 3). Riparian plots invariably lacked emergent bedrock and had no more than 1% cover of fluvial gravel, although higher cover of fluvial gravel/rock, and rarely emergent bedrock, was sometimes noted in the adjacent stream bed.

The six non-riparian *B. arnhemica* plots differed absolutely from the riparian plots in having rocky substrates, but not in slope or soil texture (Table 4). However, the range of slopes and soils appeared less than for riparian plots, non-riparian plots occurring on moderate slopes with free-draining loam or sandy-loam soils. One non-riparian plot sampled a stand on the upslope fringes of a spring-fed rain forest surrounded by eucalypt savanna, and one a vine-thicket-clad island surrounded by mangroves. The other four stands were either embedded in a rocky eucalypt savanna matrix or formed discrete sections of a larger semi-deciduous vine-thicket embedded in the rocky savanna matrix.

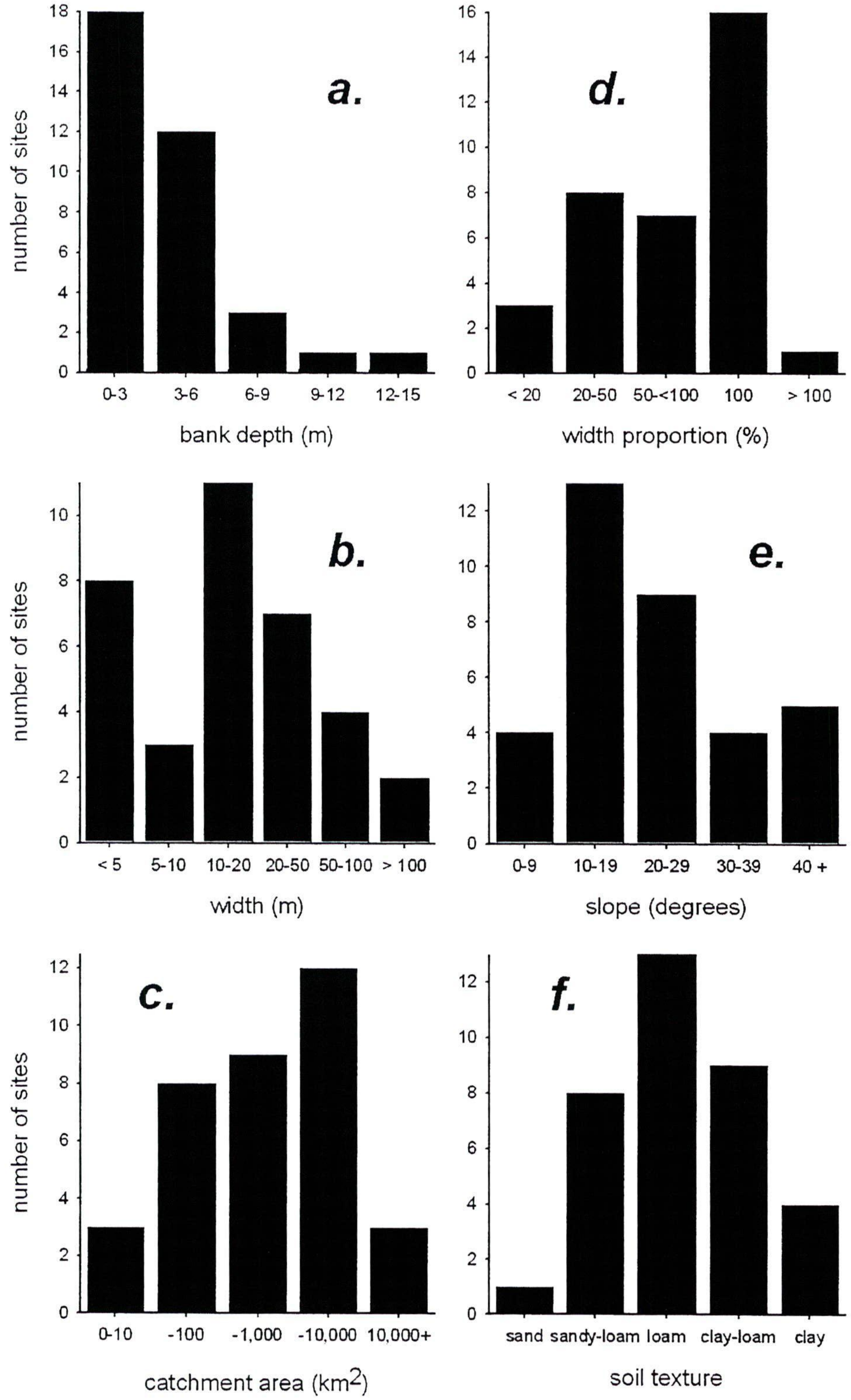


Figure 4: Physical profile of 35 riparian *Bambusa arnhemica* F. Muell. sites: *a.* & *b.* depth and width respectively of the stream bank occupied by riparian vegetation; *c.* sub-catchment area; *d.* proportion of riparian vegetation occupied by *B. arnhemica*; and e. & *f.* slope and soil texture respectively, assessed within the *B. arnhemica* plots.

Table 3: Spearman rank correlation matrix for physical characters of 35 riparian *Bambusa arnhemica* F. Muell. sites.

See Methods for details of parameters.

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ (values Bonferroni-corrected for 15 correlations).

	Width	Sub-catchment	Widthprop	Slope	Soil texture
Depth	0.515 *	0.560 **	-0.355	0.057	-0.066
Width		0.663 ***	-0.631 ***	-0.335	0.089
Sub-catchment			-0.680 ***	-0.325	0.291
Widthprop				0.187	-0.150
Slope					-0.232

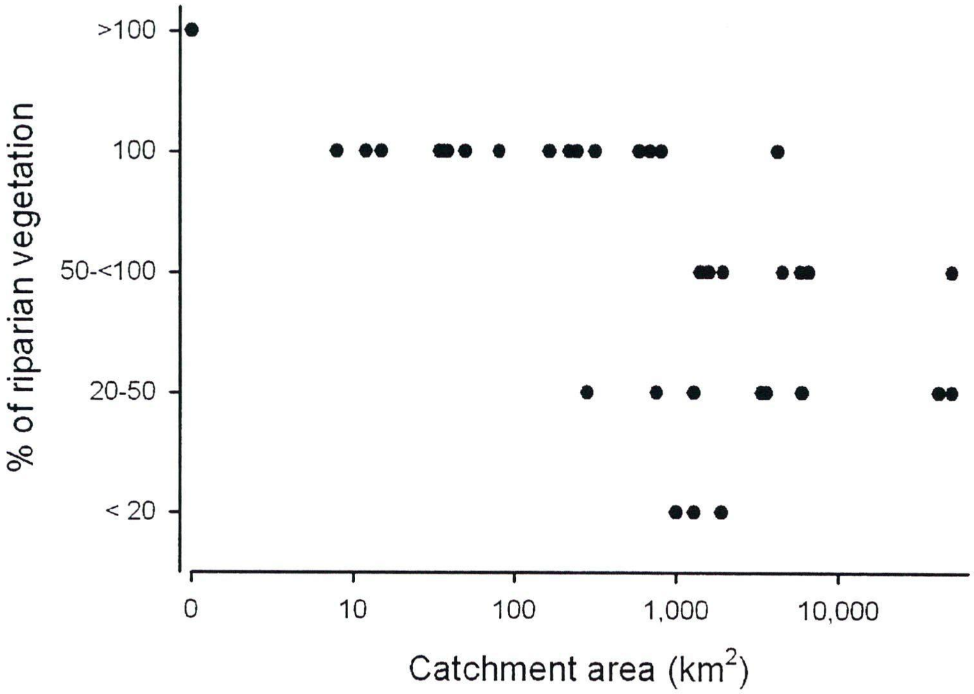


Figure 5: Relationship between catchment area and the proportion of the riparian vegetation that was occupied by *Bambusa arnhemica* F. Muell.

Table 4: Physical characters of riparian and non-riparian *Bambusa arnhemica* F. Muell. stands.

Character	Riparian (n=35) median	Riparian (n=35) range	Non-riparian (n=6) median	Non-riparian (n=6) range	Mann-Whitney *U*	Mann-Whitney (*P*)
slope (°)	20	0 – 60	17.5	7 – 25	80.5	(0.37)
rock cover (%)	0	0 – 1	43	10 – 77	0.0	(<< 0.0001)
soil texture *	3	1.5 – 4.5	3	2 – 3	69.0	(0.18)

* see Methods. Ranges from 1 = sand to 5 = clay.

Vegetation and floristics

Structurally, the vegetation in *B. arnhemica* plots comprised an open or closed forest or vine-thicket with a generally sparse shrub and forb understorey, except where *B. arnhemica* die-off had reduced the canopy and there was a parallel increase in forb cover (Table 5). Non-riparian plots tended to be more species rich, but have a lower canopy than riparian plots (Table 6).

Table 5: Vegetation structure and litter cover in *Bambusa arnhemica* F. Muell. plots not affected (n = 24) and affected (n = 17) by bamboo dieback.
"Forbs" includes *B. arnhemica* seedlings.

	Cover classes				Two-tailed	
	Mature bamboo		Bamboo die-off		Mann-Whitney	
	median	range	median	range	*U*	*P*
Canopy (> 5 m)	6	5 – 7	5	2 – 6	60	0.0001
Shrub layer (< 5 m)	3	1 – 6	3	0 – 5	189	0.69
Forbs	2	0 – 5	6	1 – 7	37.5	0.00001

Table 6: Comparison of selected attributes of riparian (n = 35) and rocky non-riparian (n = 6) *Bambusa arnhemica* F. Muell. plots.

The test statistic is the two-tailed Mann-Whitney *U* test.

	Riparian forest		Rocky non-riparian		
	median	range	median	range	*P*
Canopy height (m)	17	6 – 25	13.5	5 – 18	0.048
Plant species richness					
- all species	17	5 – 26	22.5	14 – 28	0.051
- species with cover > 1%	11	3 – 20	14	11 – 23	0.11

A total of 168 vascular plant species were recorded in the 41 *B. arnhemica* plots, but species turnover was high (Table 7*a*). Of the 65 species recorded in more than two plots, 55 (85%) were regarded as rain forest species by Liddle *et al.* (1994), the percentage increasing to 100% when only those recorded in more than 25% of plots are considered, a relationship reinforced by the prevalence of rain forest shrub, rain forest tree and woody vine life forms (Table 7*b*). Sixteen (28%) of the trees, shrubs or vines present in more than two plots were deciduous.

Classification and ordination of floristic data and site attributes revealed few informative trends (not shown). The *a priori* distinction between riparian and non-riparian sites was supported (MRPP, $T = -7.0$, $P << 0.0001$), but only the five inland non-riparian sites aggregated and there was considerable overlap in species composition (Table 7). In an ordination of life-forms (Fig. 6), the *a priori* distinction between riparian and non-riparian sites was also supported (MRPP, $T = -3.32$, $P = 0.005$). Figure 6*b* demonstrates complex gradients involving both non-riparian and riparian elements, but there were no significant site attribute correlates after Bonferroni correction. Based on the documented floristic associates, *B. arnhemica* is a component of the abundant Northern Territory monsoon rain forest groups 9 & 10 of Russell-Smith (1991). These groups are both seasonally dry, semi-deciduous and coastal or sub-coastal, group 9 being non-riparian and group 10 riparian.

Table 7: Plant species and life forms present in more than 25% of 41 *Bambusa arnhemica* F. Muell. plots.

r = riparian; rnr = rocky non-riparian. * = exotic species.

Species / life form	No. of plots	Median cover class all plots	Median cover class where present
a. species			
Bambusa arnhemica F. Muell. (Poaceae) (r,rnr)	41	5	5
Acacia auriculiformis A.Cunn. ex Benth. (Mimosaceae) (r,rnr)	32	2	3
Barringtonia acutangula (L.) Gaertn. (Lecythidaceae) (r)	22	1	2
Flacourtia territorialis Airy Shaw (Flacourtiaceae) (r,rnr)	22	1	1
Gymnanthera oblonga (Burm.f.) P.S.Green (Asclepiadaceae) (r)	17	0	1
Diospyros calycantha O.Schwarz (Ebenaceae) (r,rnr)	16	0	2
Strychnos lucida R.Br. (Loganiaceae) (r,rnr)	16	0	2
Nauclea orientalis (L.) L. (Rubiaceae) (r)	14	0	2
Flagellaria indica Willd. (Flagellariaceae) (r,rnr)	13	0	2
Lophostemon grandiflorus (Benth.) Peter Wilson & J.T.Waterh. (Myrtaceae) (r)	13	0	3
Smilax australis R.Br. (Smilacaceae) (r,rnr)	13	0	1
Elaeocarpus arnhemicus F.Muell. (Elaeocarpaceae) (r,rnr)	12	0	1
Ficus racemosa L. (Moraceae) (r,rnr)	12	0	2
Ficus scobina Benth. (Moraceae) (r,rnr)	12	0	1
**Passiflora foetida* L. (Passifloraceae) (r,rnr)	12	0	1.5
Bridelia tomentosa Blume (Euphorbiaceae) (r,rnr)	11	0	2
b. life forms			
bamboo	41	5	5
rain forest shrubs	40	3	3
Acacia	34	2	3
rain forest trees with mesophyll or larger leaves	34	3	3
other forbs (i.e. non-climbing dicotyledons)	32	1	1
herbaceous creepers	31	1	1
grass	30	2	2
woody vines	29	1	2
rain forest trees with notophyll or smaller leaves	28	2	3
eucalypts (*Eucalyptus* and *Corymbia*)	21	1	2
Lophostemon	14	0	2.5
Melaleuca	14	0	3
ferns	12	0	1

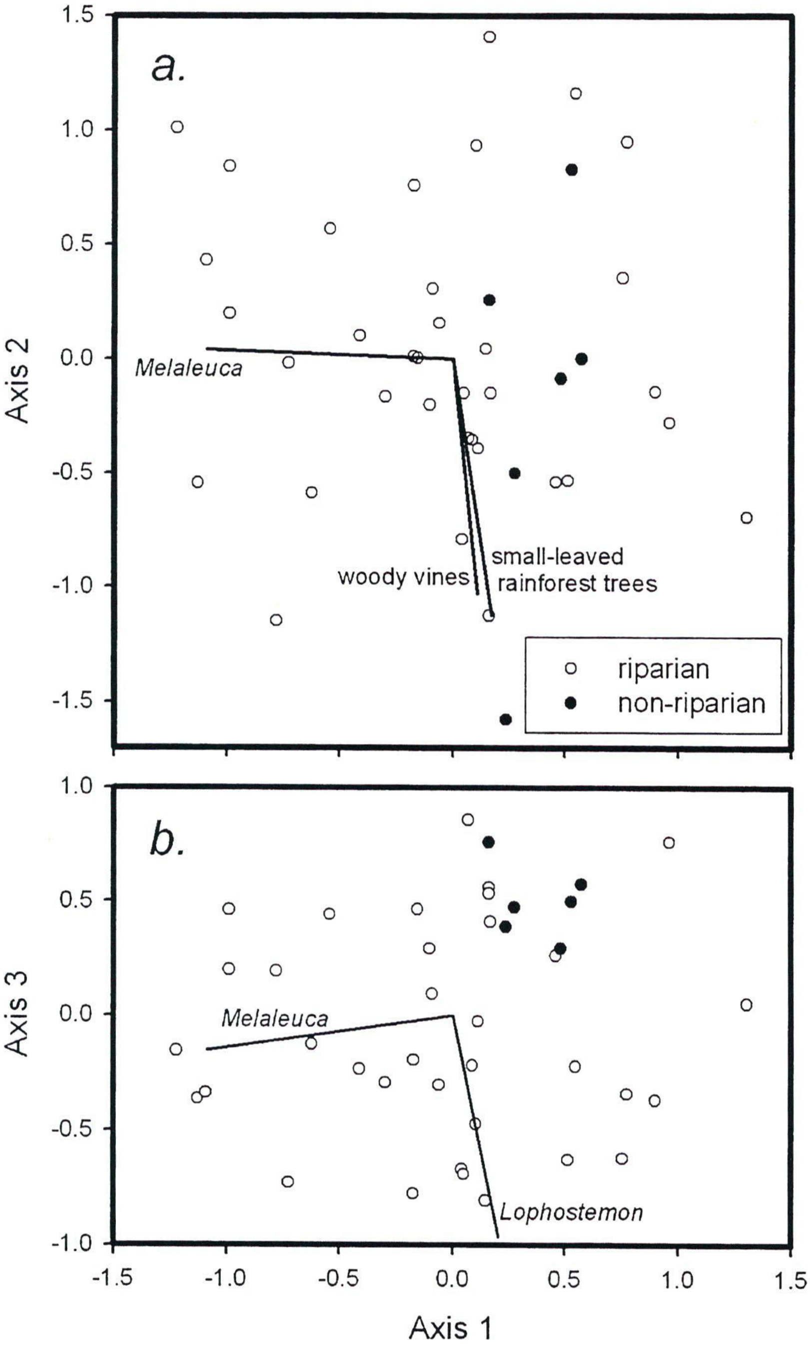


Figure 6: Three-dimensional ordination of *Bambusa arnhemica* F. Muell. plots on life form cover.

The significance of vectors has been assessed using a Bonferroni correction for 19 life forms and separately for five site attributes (none of the latter were significant). The vectors radiate from the ordination centroid in the direction of strongest positive correlation, and their length is a relative measure of the explanatory power (r^2) of the correlation. Vectors for the riparian trees *Melaleuca* (r = 0.55) and *Lophostemon* (r = 0.49) presumably corresponding to high and low levels of dry-season moisture respectively.

Vertical distribution on stream banks

On smaller watercourses, *B. arnhemica* formed or was a component of gallery forests embedded in the eucalypt savanna. On larger watercourses, it occupied discrete zones within gallery or riparian/floodplain forest complexes. Where such zonation occurred, *B. arnhemica* usually occurred upslope of riverine *Melaleuca*-dominated open forest. Upslope vegetation (sometimes on backslopes, but the term "upslope" is used throughout) from the *B. arnhemica* zone was most often eucalypt savanna but sometimes semi-deciduous vine-thicket or floodplain forest or grassland (Fig. 7*a*, Table 8).

The zones containing *B. arnhemica* contrasted strongly with adjacent vegetation (including eucalypt savanna) as indicated by analysis of life form cover (Fig. 7*b*, Table 8), the boundaries being mostly quite abrupt (Fig. 8). The zones differed somewhat in the cover and height of the canopy along a gradient downslope > *B. arnhemica* > upslope, did not differ in shrub cover or height, but differed markedly in that the upslope vegetation had a taller and denser forb layer (Table 8). Litter cover was highest in the *B. arnhemica* zone and lowest downslope (Table 8).

As in *B. arnhemica* plots, both downslope riparian forest and upslope or overbank vegetation occurred on deep alluvial soils with the sole exception of one site on Melville Island. There was weak overall tendency for riparian sites to be on steeper slopes than non-riparian sites, but no significant relationship with soil texture (Fig. 7*b*). However, analyses of matched pairs of sites revealed significant differences between *B. arnhemica* plots and adjacent upslope plots in soil texture (Wilcoxon $T = 55.5$, n = 35, $P = 0.037$) and especially slope (Wilcoxon $T = 5.5$, n = 35, $P << 0.001$). Upslope plots had finer-textured soils, whilst *B. arnhemica* plots were steeper. There were no significant difference between *B. arnhemica* and adjacent downslope plots in either slope (Wilcoxon $T = 31.0$, n = 15, $P = 0.18$) or soil texture (Wilcoxon $T = 19.5$, n = 15, $P = 0.13$).

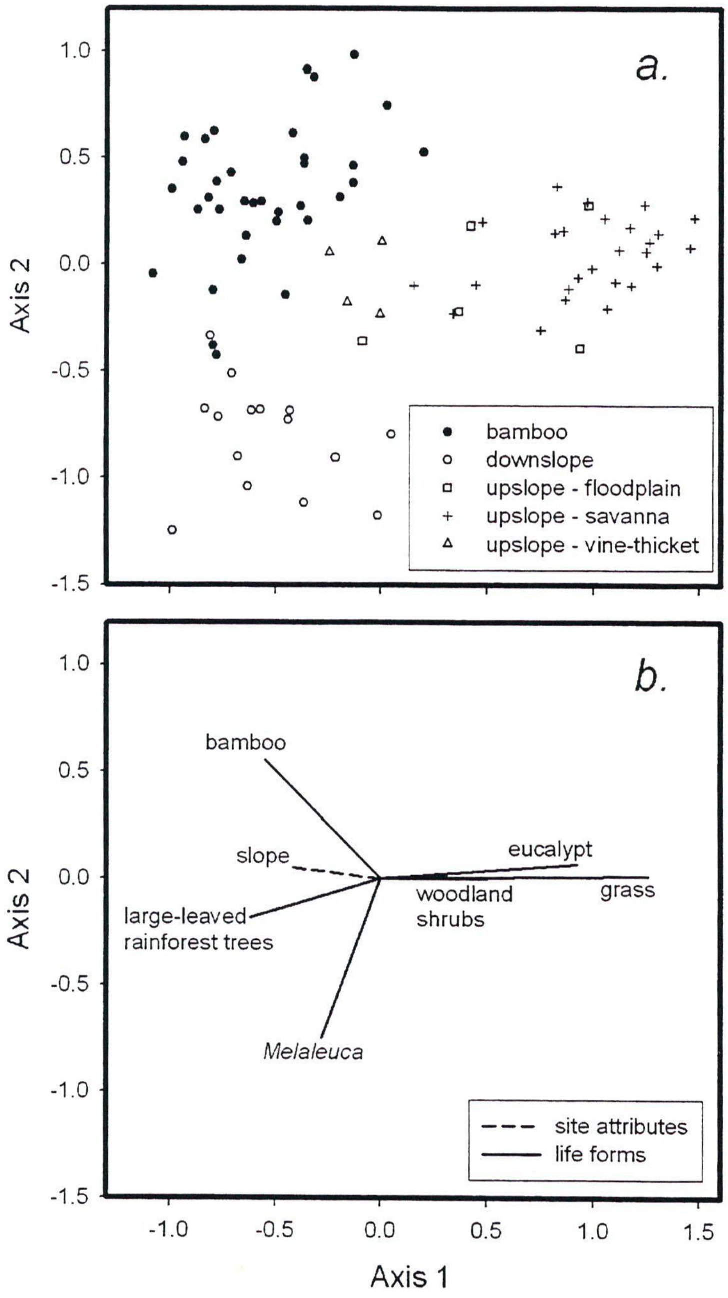


Figure 7: *a.* First two axes of a three-dimensional ordination of riparian *Bambusa arnhemica* F. Muell. and adjacent plots on life form cover, and *b.* significant life form and site attribute vectors.

The five *a priori* groups differ significantly in their ordination positions (MRPP, $T = -28.2$, $P \ll 0.001$). The significance of vectors in *b.* has been assessed with a Bonferroni correction for 19 life forms and separately for two site attributes. The vectors radiate from the ordination centroid in the direction of strongest positive correlation, and their length is a relative measure of the explanatory power (r^2) of the correlation. Significant correlation coefficients range from slope ($r = 0.30$) to grass ($r = 0.84$).

Table 8: Vegetation structure of riparian *Bambusa arnhemica* F. Muell. and adjacent downslope and upslope plots, and cover of the life forms that differentiate them (from Fig. 7*b*).

% = percent of plots present (life forms only). No of plots: *B. arnhemica* = 35; downslope = 15; upslope = 35.

Stratum / life form	*B. arnhemica* vegetation			Downslope vegetation			Upslope vegetation			Kruskall-Wallis *P*
	median	range	%	median	range	%	median	range	%	
Structural layer cover class										
tree	6	2 – 7		5	5 – 7		5	0 – 7		< 0.0001
shrub	3	0 – 5		2	0 – 6		3	1 – 6		0.46
forb	2	0 – 7		2	0 – 6		7	0 – 7		< 0.0001
litter	7	5 – 7		5	3 – 7		7	2 – 7		0.006
Canopy layer height (m)										
tree	17	6 – 25		20	6 – 27		15.5	7 – 27		0.0027
shrub	2	1 – 5		3	0.3 – 5		3.0	2 – 5		0.18
forb	0.5	0.1 – 2		0.2	0.1 – 2		1.0	0.1 – 3		< 0.0001
Life form cover class										
bamboo	5	2 – 7	100	0	0 – 4	27	0	0 – 2	20	
Melaleuca	0	0 – 5	40	5	0 – 6	93	0	0 – 5	26	
broad-leaved rain forest trees	3	0 – 6	83	3	1 – 6	100	0	0 – 5	43	
woodland shrubs	0	0 – 3	17	0	0 – 2	7	1	0 – 4	66	
eucalypts	0	0 – 4	49	0	0 – 2	7	4	0 – 5	89	
grass	2	0 – 6	77	1	0 – 5	80	7	0 – 7	97	

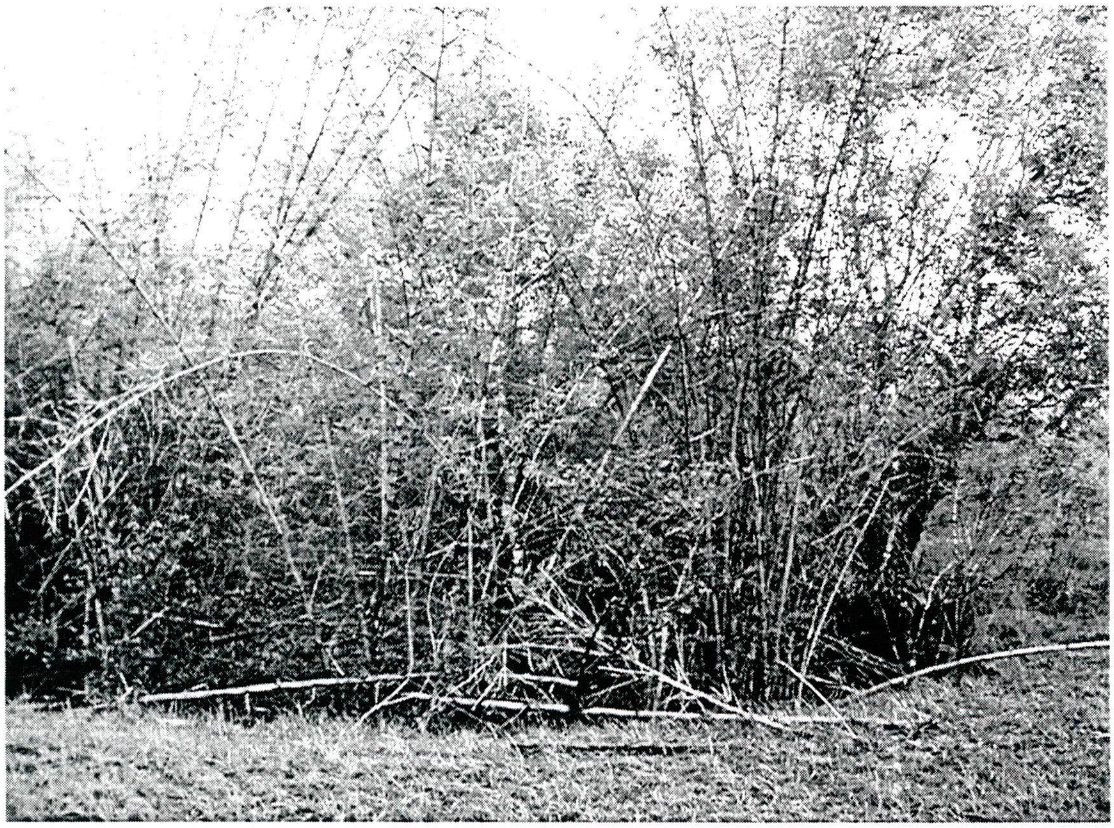


Figure 8: Bamboo (*Bambusa arnhemica* F. Muell.) stand along a small watercourse, Melville Island, showing the abrupt boundary with the adjacent savanna. Photographed during the early wet season, the adjacent savanna was burnt during the previous dry season, removing the grass biomass. The transition is associated with an abrupt change in slope. Photo: Craig Hempel.

Absence

Of 54 assessed riparian sites lacking *B. arnhemica*, 33 (61%) were judged to be clearly outside the environmental envelope of *B. arnhemica*. Seven of the 33 were rocky, 21 had *Melaleuca* or *Melaleuca* fringed with *Lophostemon* throughout the gallery forest, one had other evidence of poor drainage throughout, and four lacked any form of gallery forest, the savanna extending to the water's edge. On the remainder, some appeared suitable for *B. arnhemica* in having a well-drained alluvial bank clad with woody vines and/or scattered rain forest/vine-thicket trees, whilst some were marginal with only a limited area of well-drained alluvial bank supporting few or no rain forest/vine-thicket species.

Extensive rock along watercourses in the catchments occupied by *B. arnhemica* is generally confined to upland areas such as the sandstone ranges of the Arnhem Land and Litchfield escarpments, and to a few discrete granitic areas along the inland fringe of the species' range. Although *B. arnhemica* was not recorded in any of these areas, distinguishing the direct effect of the presence of rock from the soil properties associated with these parent materials is difficult. However, direct evidence of aversion to rockiness was obtained at Middle Creek in the Daly River catchment, where limestone rock outcrops occurred interspersed with and downstream of *B. arnhemica* stands (Fig. 9). At Middle Creek, the dissociation of *B. arnhemica* seedlings and rock was strong (Fisher's Exact Test $P = 0.005$), the only co-occurrence being when rock cover was less than 1%. In contrast, there was no significant relationship between rock cover and the cover of woody riparian vegetation.

Compared to a sample of sites with *B. arnhemica* matched in having a discrete gallery forest embedded within eucalypt-dominated savanna and not associated with the coastal floodplain, gallery forests dominated by *Melaleuca* spp. tended to occur on smaller sub-catchments, generally less than 1,000 km^2, and after correction for catchment area, had significantly lower bank profiles (Fig. 10).

Along the sub-coastal floodplain of the Adelaide River, the only mainland situation where riparian *B. arnhemica* occurred upslope from mangroves, stands toward the downstream limit of *B. arnhemica* were entirely confined to the western, fire-sheltered bank (Fig. 11).

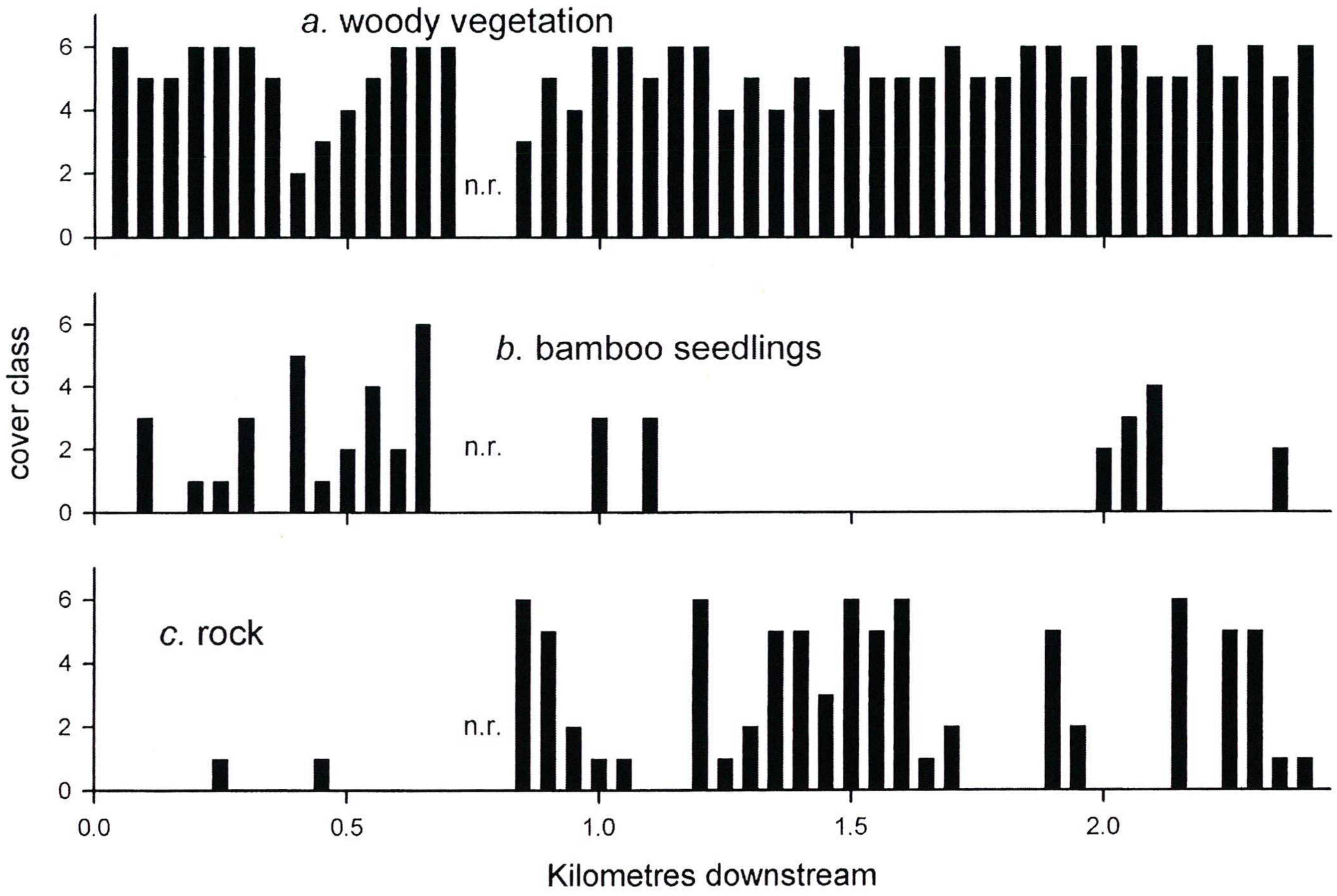


Figure 9: Relationship between riparian vegetation and rock cover along lower Middle Creek (13°49'S, 131°20'E). The rocks are Cambrian limestones. n.r. = no record for two adjacent segments due to disturbance associated with a bridge. The cover of bamboo (*Bambusa arnhemica* F. Muell.) seedlings was significantly negatively correlated with that of rock (r_s = -0.53, n = 46, $P < 0.001$), but that of woody vegetation was not (r_s = -0.19, n = 46, $P = 0.20$).

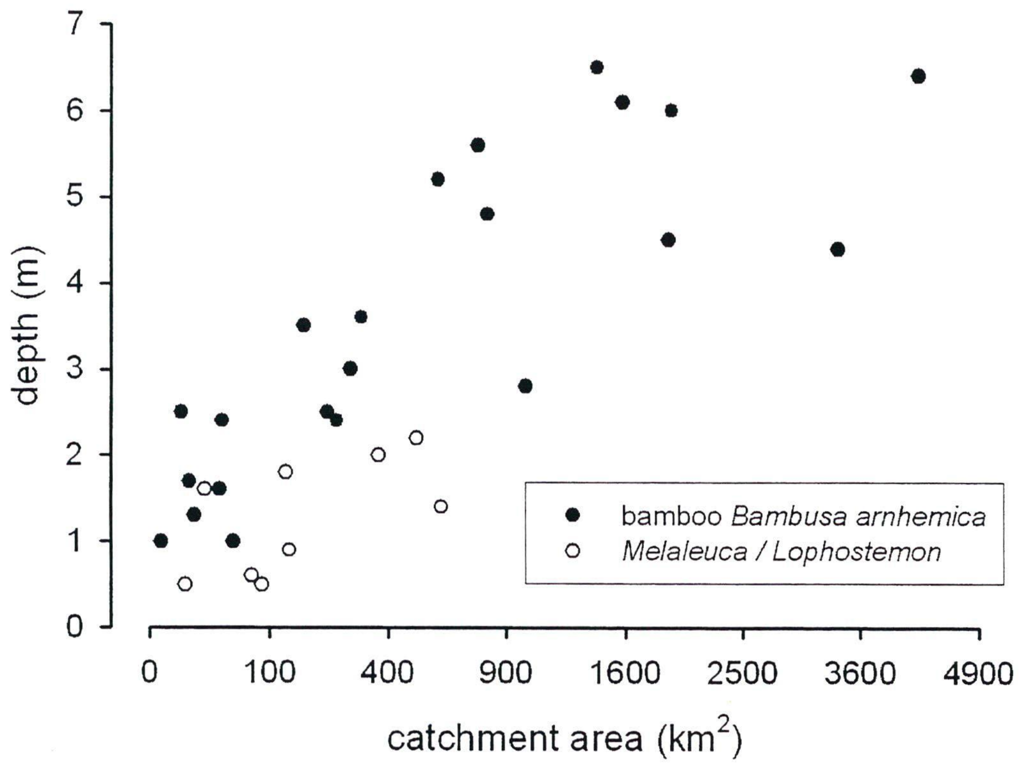


Figure 10: Relationship between the depth of riparian vegetation, catchment area and riparian vegetation-type.

All sites are on main watercourses and backed by savanna vegetation. "Bamboo" sites are those at which *Bambusa arnhemica* F. Muell. was present, whereas at "*Melaleuca*/*Lophostemon*" sites, *B. arnhemica* was absent and *Melaleuca* sp. (see text) occurred throughout the riparian profile or with a narrow fringe of *Lophostemon lactifluus* (F.Muell.) Peter Wilson & J.T.Waterh.. *B. arnhemica* sites on the Daly River have been excluded as outliers (catchment > 40,000 km^2) likely to exercise undue leverage on analysis. Both catchment area and vegetation types were significant effects (ANCOVA, catchment area square-root transformed, F_1 = 54.6, 14.4 respectively, *P* both < 0.001).

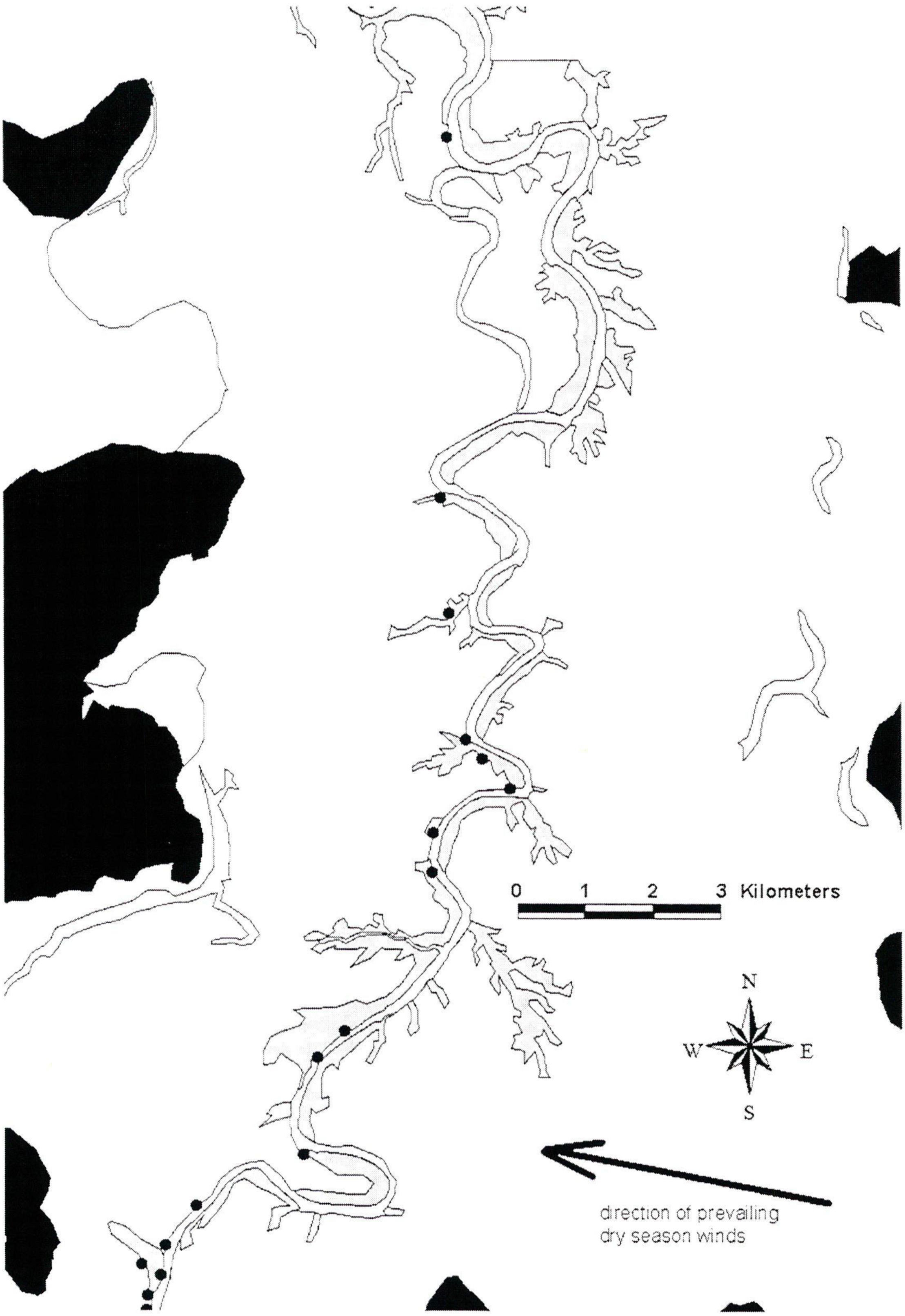


Figure 11: Downstream occurrence of *Bambusa arnhemica* F. Muell. (black dots) on the tidal section of the Adelaide River floodplain, showing confinement to the western bank.

Grey patches are mangroves lining the River and black patches are non-floodplain areas.

Discussion

Bambusa arnhemica has a sharply circumscribed global distribution, a decidedly patchy distribution within catchments, and occupies distinct vertical zones on river banks. Vertical zonation is readily explicable in terms of edaphic and environmental constraints (below) and can scarcely be related to dispersal limitations. But given the species' considerable flexibility with regard to moisture regime, stream type and parent material, its distribution at larger scales is not so readily understood. Its occurrence on rock and sandy substrates at non-riparian sites, but evident avoidance of these substrates along watercourses, is a conundrum requiring explanation. Though restricted to a region of fairly high but intensely seasonal rainfall and unremittingly high temperatures, similar conditions prevail over substantially greater areas along the north coast of the Northern Territory. Numerous other sub-coastal lowland rain forest species in the Northern Territory are mostly much more widely dispersed (Liddle *et al.*, 1994). For example, *Flacourtia territorialis*, a species that commonly co-occurred with *B. arnhemica* (Table 7) and which is also a Northern Territory endemic, extends a little further inland and 480 km further to the east. The few exceptions are narrow endemics, for example *Burmannia* sp. D161177 and *Vernonia patula* (Fensham, 1993; Liddle *et al.*, 1994). One possible explanation is that *B. arnhemica* is a relatively recent arrival in Australia that has yet to occupy its full potential range. Here, we consider edaphic, environmental and dispersal influences and assess their historical biogeographic implications.

The moisture paradox

We did not locate *B. arnhemica* on soils perennially moistened by springs. It was not obligately associated with flood-prone environments and exhibited considerable tolerance of intense seasonal drought, the species being facultatively deciduous (Franklin, unpubl. data). It was uncommon to scarce on the low-lying coastal floodplain, where it was associated with raised levees, although high fire frequencies (Gill *et al.*, 2000; Lawson, 2000) may also impose limits in that environment. It did not generally occur on small watercourses with a low bank profile, nor generally on the downslope portion of the banks of larger rivers, in both situations being replaced by *Melaleuca* forest. *Melaleuca leucadendra* (L.) L. and *M. cajaputi* Powell are the most inundation-tolerant of trees on floodplains and riverbanks in northern Australia (Bowman & McDonough, 1991; Cowie *et al.*, 2000), often remaining under water well into the dry season (Williams, 1979; pers. obs). The fire-tolerance of riparian *Melaleuca* spp. (pers. obs.) may be a factor in dominance at some sites, but cannot explain their frequent replacement of *B. arnhemica* downslope on river banks. It seems unlikely that *B. arnhemica* was excluded from more flood-prone sites by competition with *Melaleuca*. Riparian vegetation systems subject to disturbance by floodwaters tend to be disclimax communities with opportunities for colonisation by edaphically-tolerant species (e.g. Pettit *et al.*, 2001), and the downslope riparian communities in this study did not always feature high abundance of *Melaleuca*.

Stream turbulence and the associated erosive force poses a particular problem for seedlings of riparian plants (Gregory *et al.*, 1991; Gurnell, 1997; Karrenberg *et al.*, 2003). Bamboos lack tap roots and may thus be particularly vulnerable to turbulence promoted by rock outcrops within watercourses, and also to the restricted rooting opportunities associated with surface or near-surface bedrock. *Bambusa arnhemica* also did not occur on the sandiest of stream banks where stability for seedlings may also be a problem.

These lines of evidence suggest a preference for lentic riparian systems but also an intolerance of poor drainage during the dry season, a somewhat restraining combination. Intolerance of poor drainage by *B. arnhemica* during the dry season is somewhat paradoxical given that *B. arnhemica* not only tolerates inundation for two or more months of the year as both mature clumps and seedlings (Franklin & Bowman, 2003), but that growth in the form of rapid elongation of culms occurs during the mid- to late-wet season when riparian stands are subject to inundation (Franklin, unpubl. data). It maybe that soil and plant aeration is necessarily restored during the dry season, aerial roots and hollow internodes providing access to or reservoirs of oxygen during inundation (Cowie *et al.*, 2000; Franklin, 2003*a*).

Fire and soil fertility

Riparian *B. arnhemica* occurred only on deep alluvial soils, whilst the soils of rocky hillside sites are all free-draining, ferrugineous, and of moderate fertility notwithstanding the diversity of parent materials (P. Ferenczi pers. comm.). However, absence from infertile savanna laterites and sands could be attributable to the high frequency of fires in those environments. Occasional occurrence on coastal sands is problematic for any notion of absolute avoidance of infertile soils.

The transition from *B. arnhemica* gallery forests to upslope savannas was mostly abrupt, but both vegetation types occurred on deep Quaternary alluvium. The transition intersected gentle gradients in soil texture (this study) and flood frequency (Franklin & Bowman, 2003), but was generally more or less coincident with the lip of the stream bank. Although in a matched-pairs analysis the savannas occupied soils of finer texture, the range of textures overlapped extensively, suggesting that the textural difference was a consequence of depositional patterns and not a contributor to the vegetation transition.

We suggest, therefore, that direct edaphic exclusion of *B. arnhemica* from savannas growing on fertile soils is unlikely, and that a fire-vegetation cycle must be invoked to explain the boundary. Grass cover was more or less continuous in the savanna but scarce in the gallery forests where litter was the most obvious fuel. Although litter fuels in monsoon or gallery forests may contribute as much dry weight as the grass fuels in adjacent savannas, the former retain more moisture and may thus be less prone to fire particularly early in the dry season (Bowman & Wilson, 1988; Biddulph & Kellman, 1998). The position of gallery forests upslope from water or streambeds and downslope from the main fire-prone matrix doubtless also contributes to reduced fire frequencies. In a range of environmental settings, fire frequency and/or intensities tend to be lower in riparian forests than adjacent vegetation (e.g. Stott, 1986; Kellman *et al.*, 1998; Beaty & Taylor, 2001; Russell & McBride, 2001; Everett *et al.*, 2003). Lower fire frequencies permit the development of less fire-tolerant vegetation (Kellman *et al.*, 1998) which may itself retard fire or, by dent of greater canopy closure, suppress grass fuels.

Although *B. arnhemica* seedlings are remarkably tolerant of fire (Franklin & Bowman, 2003), mature clumps are less so (Franklin, unpubl. data), possibly reflecting perennial commitment in mature clumps to above-ground biomass which is exposed to fire. *Bambusa arnhemica* is somewhat fire-retardant, and fires may stop upon reaching the edge of *B. arnhemica* stands. We have previously proposed that *B. arnhemica* occupies somewhat fire-protected locations and that its capacity to cope with fire is positively related to soil fertility (Franklin & Bowman, 2003). Additional direct evidence of a fire-refugial distribution garnered in the course of this study is two-fold. At its downstream distributional limit on the Adelaide River floodplain levee, *B. arnhemica* was confined to the western side of the river where it is sheltered by the river from the prevailing east-south-easterly dry season winds (Gill *et al.*, 1996) that have driven frequent floodplain fires under both recent and pre-European management regimes (Gill *et al.*, 2000; Lawson, 2000). Secondly, inland non-riparian stands of *B. arnhemica* were mostly associated with rock outcrops, a situation where localised fire protection is a feature (Price *et al.*, 2003). A relationship between fire tolerance and soil fertility is suggested by the occurrence of *B. arnhemica* on coastal, but not inland sandsheets.

Dispersal, environment and patchiness

A recurrent theme in the patterns of distribution documented in this study is that *B. arnhemica* occurred more or less continuously along watercourses from a sharply-defined upstream limit downstream to the poorly-drained coastal plain. This is particularly evident in the greater detail available in Fig. 3. The upstream limits varied by orders of magnitude between catchments and sub-catchments, with *B. arnhemica* apparently altogether absent from some sub-catchments within its general range. Notwithstanding its flexibility with regard to parent materials, *B. arnhemica* also occurred only infrequently in non-riparian seasonally dry "rain forests", the species being too uncommon to feature in Russell-Smith's (1991) floristic key to Northern Territory rain forests. The distribution of *B. arnhemica* may thus be the product of infrequent and incomplete dispersal between catchments and to non-riparian sites, followed by passive and thus unidirectional water-borne dispersal. According to this scenario, occurrence at the level of sub-catchments and especially in the upper reaches may be quite idiosyncratic.

There are a number of considerations that may impact on this hypothesis. Seemingly idiosyncratic upstream distribution limits could also be attributable to changes in the geology or structure of the watercourse that may render them unsuitable for *B. arnhemica*. A number of minor catchments appeared quite unsuitable for riparian *B. arnhemica* because their granitic parent material yields watercourses that are sandy and/or rocky. Tributaries of the South Alligator River on the eastern side arise from the extensively-rocky Arnhem Land Plateau. Smaller spring-fed watercourses on sand sheets and some other geomorphic forms lacked the longitudinal and/or lateral slope and/or erosive force to create well-drained, incised banks. Several minor exceptions to continuity of riparian distribution, in the form of gaps of 1–5 km, appear readily attributable to either poor drainage or rockiness along the watercourse. In a number of cases, however, including a major portion of the Daly River, we are unable to rule out the possibility that absence was attributable to dispersal limitations.

The major exception to continuity was the 30 km break in distribution on the Finniss River, but this may be explicable within the general framework proposed. The small headwater stand on the Finniss River flowered in synchrony with *B. arnhemica* in the headwaters of adjacent catchments, but two years prior to the more extensive downstream stand, suggesting that the upstream stand may be the result of recent dispersal from nearby catchments. Both the anomalous distribution and the spatio-temporal patterns of flowering involved are documented in Franklin (in press).

Although firm evidence is lacking, we consider it likely that most passive dispersal of *B. arnhemica* is by seed rather than vegetative material, although the downstream dispersal of exotic bamboos in Puerto Rico was attributed to culm breakage during storms and subsequent re-rooting (O'Connor *et al.*, 2000). Healthy *B. arnhemica* culms and branches are particularly tenacious (Franklin, pers. obs.). Furthermore, vegetative dispersal is unable to explain dispersal across catchment boundaries and to non-riparian sites. The lack of obvious adaptation to enhance dispersal in the seed of *B. arnhemica* is typical of many bamboos (Judziewicz *et al.*, 1999) but somewhat unusual amongst grasses (Davidse, 1987). Van der Pijl (1982) suggested that the primary seed dispersal mechanism among bamboos was "dyszoochory", in which seed is dispersed only occasionally and accidentally by consumers who normally destroy the seed. Infrequent seed dispersal may be compounded both by the small suitable "target" area for deposition of seeds in the savanna matrix, and infrequent seed production. *Bambusa arnhemica* is gregariously semelparous and populations flower no more than once every 40 years (Franklin, in press). On the other hand, seed production can be extraordinarily prolific during a mass-flowering event (Franklin, in press).

Limited dispersal capacity in bamboos may be inextricably linked to the unusual life histories of semelparous species, in which local domination of space permits the creation and control of regeneration space by parental death. In rain forest environments, this is a striking variation of the role of canopy gaps for light-dependant seedlings. If so, this represents an extreme case of dispersal being disadvantageous because the site has proven successful for the parent (Cheplick, 1992). Patchy monodominance may simply be a product of limited dispersal or, via "neighbourhood selection" (Wilson, 1987), an evolutionarily viable option for enhancing parental control of space. Dyszoochory can be interpreted as an extreme dispersal dimorphism (van der Pijl, 1982), which Cheplick (1992) argued should be favoured under the intense sibling competition that must arise with limited dispersal.

Historical biogeography

Bambusa arnhemica is an endemic species with no obvious adaptation to dispersal (Franklin, 2003*a*), is well-established in numerous tributaries of a number of catchments (this study), and has a well-developed flowering wave (Franklin, in press). It is thus likely to have been established in northern Australia for a considerable period of time. On the other hand, dispersal appears incomplete, there is no evidence of speciation (Franklin, 2003*a,b*), and the species is not known to support any endemic fauna (see in particular Woinarski *et al.*, 2000). The lack of an endemic fauna stands in strong contrast to bamboo in Asia (Carter *et al.*, 1999; Wei *et al.*, 2000; Pradhan *et al.*, 2001), South America (Stallings *et al.*, 1994; Kratter, 1997) and Madagascar (Tan, 1999). Several considerations frame speculations about the "intermediate" time frames involved.

The region occupied by *B. arnhemica* has a long history of geological stability (Williams, 1991), but has been subject to major aridity phases and coastline retreat during the Pleistocene (Nix & Kalma, 1972; Voris, 2000). The rain forest flora was subject to one or more bottlenecks during arid phases, but has recently expanded (Shapcott, 1998, 1999, 2000). Whether and how riparian *B. arnhemica* would have been affected by this is unclear, but the possibility that the current range is substantially a product of Holocene expansion must be considered plausible. It is also possible that the extensive and rocky Arnhem Land Plateau and its northward extension to the poorly-drained coastal plain has provided a barrier to eastward expansion.

Regardless of timing, that synchronous flowering occurs in discrete patches, some of which dissect adjacent streams perpendicular to the direction of flow (Franklin, in press) suggests that the flowering wave of *B. arnhemica* has been largely superimposed on an established distribution.

Acknowledgements

This work was funded by the Parks & Wildlife Service of the Northern Territory. For their assistance in the field, I am grateful to Markwell Drury, Ron Felzer and Christine Maas. Staff of the Darwin Herbarium, and especially Chris Mangion and Bob Harwood, gave generously of their time and expertise to assist with identifications. Greg Connors, Chris Mangion and Craig Hempel provided databases of *B. arnhemica* location records. Phil Ferenczi provided extensive guidance with the interpretation of parent materials and soils. Guy Boggs guided the digital calculation of catchment areas, and Dan McIntyre assisted extensively with the preparation of maps. A number of landholders and management agencies kindly gave permission to work on their land.

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Chapter 4:

Fire, flood and regeneration

This chapter has been published as:

Franklin DC, Bowman DMJS. 2003. Bamboo, fire and flood: regeneration of *Bambusa arnhemica* (Bambuseae: Poaceae) after mass-flowering and die-off at contrasting sites in monsoonal northern Australia. *Australian Journal of Botany* 51: 529-542.

Abstract

Bambusa arnhemica F.Muell., a long-lived, gregarious-flowering and semelparous bamboo endemic to north-western Australia, occurs in remarkably disparate but somewhat fire-sheltered flood-prone riparian forest and rocky hillside vine-thickets, but not in adjacent fire-prone savannas. We investigated the response of *B. arnhemica* seedlings to fire and flood at two contrasting sites over the two-and-a-half years following a mass-flowering and die-off event. Seedlings grew vigorously notwithstanding either prolonged inundation or total loss of above-ground parts to fire within their first year. However, there was no evidence that such disturbance promoted regeneration, and several veins of evidence suggest that *B. arnhemica* is fire-retardant and refugial rather than fire-promoting. We suggest that creation of canopy gaps by parental death is a more parsimonious and generalisable hypothesis for the evolution of gregarious semelparity in bamboos than the recently-advanced *bamboo fire-cycle hypothesis*. However, both hypotheses are potentially *group selectionist*, and information about dispersal distances and/or the spatial genetics of relatedness are required to resolve the problem.

Introduction

Diversity in many tropical forests is maintained by moderate levels of disturbance from a variety of sources. In humid rainforests, canopy gaps caused by wind throw or death with age create opportunities for light-dependant regeneration (Coomes and Grubb 2000; Lewis and Tanner 2000). In deciduous or semi-deciduous monsoon forests, fire may be an important selective source of disturbance influencing regeneration (Bowman *et al.* 1990; Marod *et al.* 1999; Fredericksen *et al.* 2000; Khurana and Singh 2001). In riparian forests, inundation and disturbance by flooding is a key ecological process (Williams 1979; Oliveira-Filho *et al.* 1994; Karrenberg *et al.* 2003).

The gregarious semelparity of certain arborescent forest-dwelling bamboos (Bambuseae: Poaceae) (Janzen 1976) poses a regeneration conundrum, and it is unclear whether such species are sensitive to or favoured by disturbance. Death of the parent after a single, gregarious reproductive event is a risky reproductive strategy, exposing cohorts and even populations to the consequences of catastrophic disturbance (Young and Augspurger 1991). Infrequent reproduction appears ill-adapted to the exploitation of temporally and spatially unpredictable canopy gaps. On the other hand, parental death creates canopy gaps (Foster 1977), and bamboo seedlings are light-dependant (Tewari 1992; Banik 1997). The gregarious death of various bamboo is a major forest perturbation with critical consequences for the regeneration of many forest tree species (Marod *et al.* 1999; Abe *et al.* 2002; Gonzalez *et al.* 2002).

To explain this conundrum along with perplexing questions about the evolution of gregarious semelparity in bamboos, Keeley and Bond (1999) proposed the "bamboo fire-cycle hypothesis". According to this hypothesis, the ecological function of death after flowering is to promote wildfire, enhancing canopy gaps and favouring bamboo seedlings over those of other tree species. The hypothesis remains controversial (Saha and Howe 2001 cf. Keeley and Bond 2001), with scant evidence for its resolution. With a few notable exceptions (Soderstrom 1981; Stapleton 1998), bamboos have no obvious morphological specialisations to cope with fire (Saha and Howe 2001), although the clonal growth habit with underground rhizomes that generate culm growth buds and store nutrients, a general adaptation to coping with a range of disturbances (Trabaud 1987), may serve bamboo well in the event of fire. In the *paramos* of South America, bamboo resprouts vigorously after fire (Horn 1989; Safford 2001). Bamboo seedlings may be sensitive to fire, especially prior to the development of their first rhizomes (Banik 1990), but fire may enhance seedling survival (Gadgil and Prasad 1984). Fire may indeed be frequent following bamboo die-off (Gadgil and Prasad 1984). More generally, fire may promote invasion of broad-leaved forests by bamboo (Wong 1991; Silveira 1999; Banana and Tweheyo 2001).

Flooding might also create canopy gaps for bamboo seedlings, but it is unclear how this could be synchronised with infrequent gregarious semelparity. Bamboos are generally intolerant of water-logging (Tewari 1992). Severe flooding killed many *Bambusa* spp. seedlings (Benton and Weatherhead 1996), and Oliveira-Filho *et al.* (1994) reported that the bamboo *Merostachys neesii* was restricted to the upper parts of a Brazilian riparian forest where flooding was at most occasional.

The Top End Bamboo *Bambusa arnhemica* is a clumping, clonal, 10–20 m tall, arborescent monocotyledon. It is long-lived (estimated at 40–50 years, Franklin ms) and semelparous. Flowering occurs gregariously such that 95–99% or more of clumps flower and die synchronously in areas ranging from a few hectares to many kilometres across, with regeneration occurring freely from seed (Franklin unpubl.). The species is endemic to the higher-rainfall regions of the far north-west of the Northern Territory (Liddle *et al.* 1994; Mallett and Orchard 2002), where it occurs in riparian forests (Cowie *et al.* 2000) and much less frequently in semi-deciduous vine-thickets on rocky hillsides (Brock 1993).

Fire and flood are two potentially-catastrophic events that occur with close to annual frequency in and near environments occupied by the Top End Bamboo *Bambusa arnhemica*. The contrasting nature of the riparian and vine-thicket environments along with the absence of *B. arnhemica* from adjacent fire-prone savannas raises intriguing questions about the forces shaping its patchy distribution. In this study, we consider the possible roles of fire and flooding in shaping the local distribution of *B. arnhemica* stands. In particular, we examine a series of questions pertinent to Keeley and Bond's fire-cycle hypothesis, namely: are bamboo seedlings fire-tolerant and might any such tolerance differ with the moisture status of sites? is disturbance by fire and/or flooding critical to the regeneration process? and, is *B. arnhemica* a fire-promoting or fire-refugial species? We do so by comparing the site attributes and survival and growth of seedlings at contrasting riparian and hillside sites, and by shadehouse trial decapitation of first-year seedlings. At both sites, a gregarious-flowering event occurred in late 1999, and we follow the fate of seedlings over the ensuing two-and-a-half years.

Study areas and methods

Study sites

The two study sites, Bamboo Creek and Heathers Lagoon, are 8.5 km apart in the mid-catchment of the Adelaide River and 67 and 73 km respectively from the ocean. They were selected because of their proximity but contrasting environmental settings, and because at both sites, mass-flowering, die-off and subsequent germination of seedlings took place in 1999. The Adelaide River is central to the limited distribution of *B. arnhemica* (Liddle *et al.* 1994), and it and a number of its tributaries are lined near-continuously with stands of the species. The River is a 160 km long (direct-line distance), perennial stream of the northern coastal lowlands and foothills of the Northern Territory, sinuous and tidal for almost half its length. Flow in non-tidal reaches during the dry season is maintained at low levels by a series of springs, whilst massive fluctuations during the annual wet season result in inundation of riparian vegetation and dispersion over extensive black-soil floodplains.

The Heathers Lagoon site (12°55'S, 131°15'E) is on and adjacent to a north-facing 5 m-high bank of the Adelaide River 119 river kilometres from the sea and 2 km below the upstream limit of tidal influence. There is no evidence of salt-water effects on the riparian vegetation at the site or for about 30 river kilometres downstream. The site comprises a 30–50m wide band of 20 m tall riparian forest of *Melaleuca leucadendra* and *B. arnhemica*, and adjacent 15 m tall eucalypt savanna woodland. The latter is part of a floodplain complex that includes extensive areas of treeless grassland with embedded ephemeral and semi-permanent freshwater wetlands. Soils are deep, alluvial and often cracking black clay-loams throughout. A river depth gauge (Dirty Lagoon) situated on the same bank and 100 m downstream from the site has been maintained intermittently since 1963.

The Bamboo Creek site (12°55'S, 131°10'E) comprises a series of north-south, pyritic quartzite strike ridges of early Proterozoic origin, adjacent talus (20–35°), and a small outwash valley, 50 – 120 m above sea level. Soils are deeply ash-stained, dark silty loams throughout. A series of non-riparian bamboo and *Ficus* vine-thickets on the talus, and an evergreen rainforest patch centred on a series of perennial springs and stream in the valley, are embedded in a grassy eucalypt open forest / savanna woodland landscape (Fig. 1). *A priori* (subjective) vegetation types recognised were as follows: evergreen

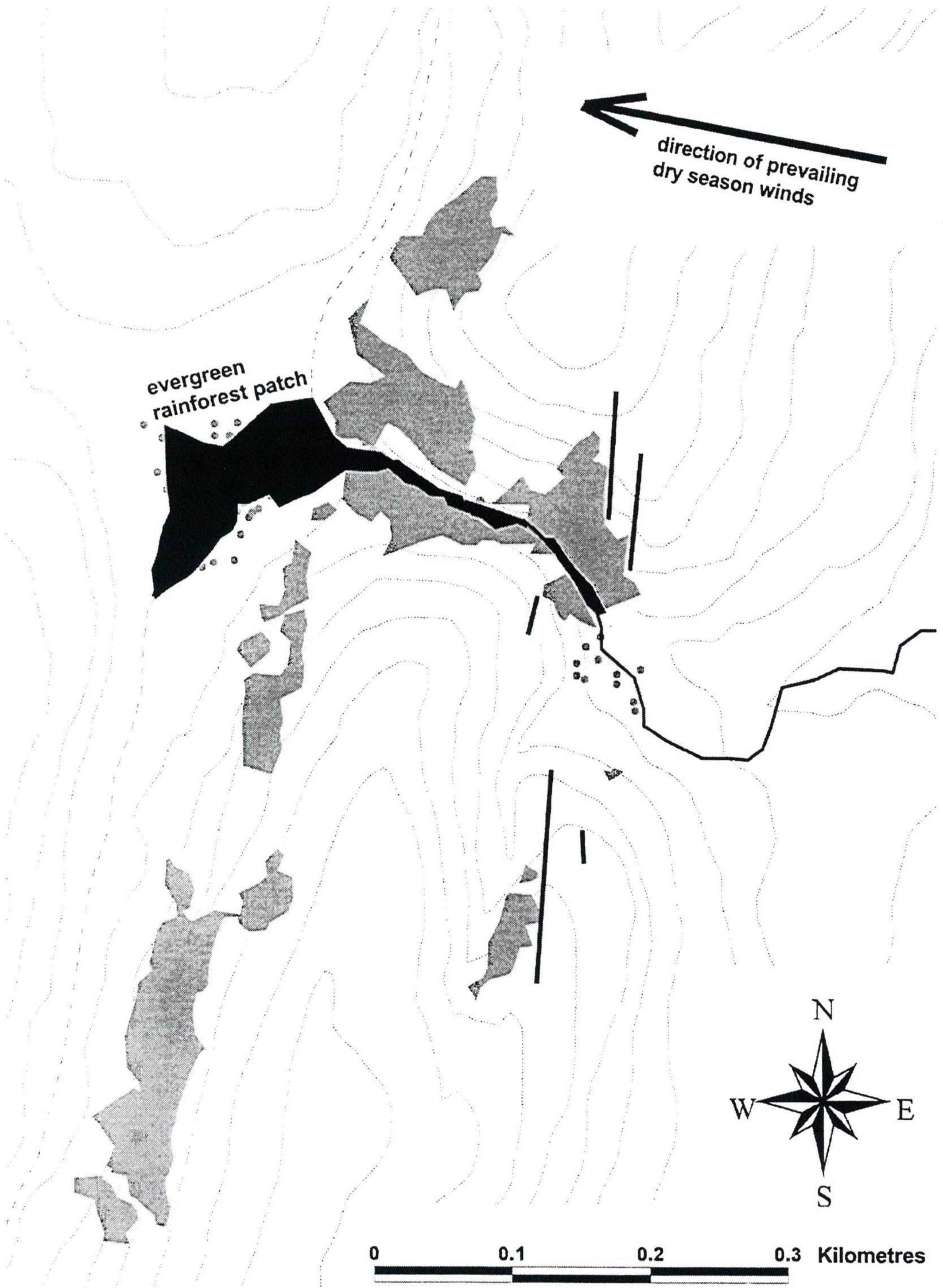

Figure 1. Distribution of *Bambusa arnhemica* stands and clumps in the greater Bamboo Creek area.

Grey patches are bamboo thickets; grey dots are isolated bamboo clumps. Straight heavy black lines are outcropping rock bars. The contour interval is 10 m. A perennial stream - Bamboo Creek - (unbroken line) and two intermittent tributaries (dashed lines), are also indicated.

rainforest, eucalypt savanna on non-rocky, more or less level ground, and an intergrading mosaic of vine-thicket and eucalypt savanna on the rocky slope.

Because of their proximity and setting in a low-lying landscape, the climate of the two sites is unlikely to differ except for some shading and solar radiation effects (Kirkpatrick *et al.* 1988) associated with the hills at Bamboo Creek. Mean annual rainfall is 1500 mm, almost all rain falling between the months of October and April inclusive. Temperatures are warm to hot throughout the year. In the dry season, the prevailing breezes blow from the east-south-east, whereas in the wet season they are more variable in direction with a predominant north-westerly (monsoonal) influence.

At both sites, almost every clump of *Bambusa arnhemica* flowered in the second half of 1999. Following flowering, seedlings germinate with the first substantial rains of the wet season, usually in October or November, and the old clumps begin senescing at about this time and usually die by the end of the wet season or shortly thereafter (Franklin unpubl. data).

Data collection

The vegetation, watercourses, rockbars and plots at Bamboo Creek were mapped by taking GPS readings at points or at 10–20 m intervals along features or boundaries. River gauge depths at Heathers Lagoon were calibrated from an external marked board on the gauge to landscape and vegetation features using a clinometer.

Marked plots were established at both sites at 50 m intervals along a series of primary transects that followed landscape contours through and adjacent to bamboo stands. At the Heathers Lagoon site, two primary transects (150 and 200 m long) containing extensive bamboo stands were placed in the lower and upper part of the riparian vegetation respectively, and a third transect (150 m) placed in adjacent savanna woodland that lacked bamboo, giving a total of thirteen plots. At Bamboo Creek, there were six primary transects and 26 plots spanning valley evergreen rainforest, bamboo vine-thicket on adjacent rocky slopes, and savanna vegetation both up- and along-slope from the bamboo stands (Fig. 2).

Plots were 20 by 10 m, with their longer central axis along the primary transect. Within each plot, a 10 m secondary transect was established centrally along the contour.

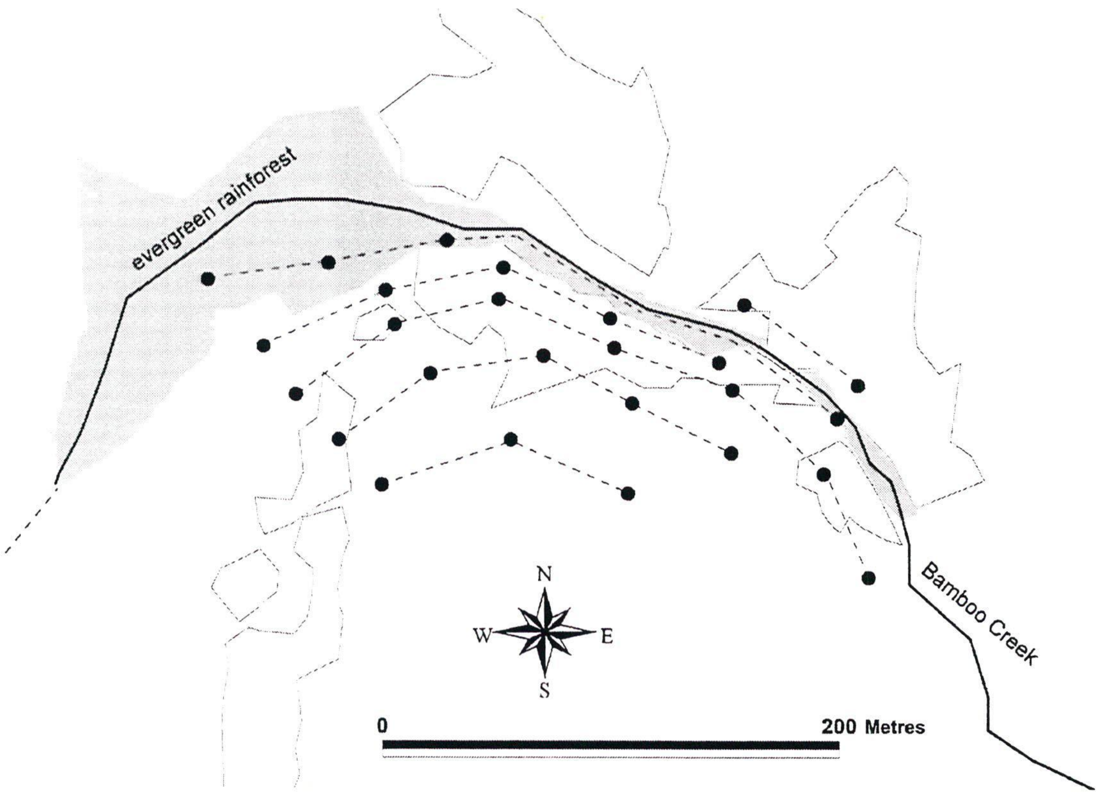

Figure 2. Distribution of transects (dashed lines) and plots (dots) at the Bamboo Creek study site.

Outlined areas are mono-dominant bamboo stands.

Plots were established at the end of the 2000 dry season. The extent of fire was assessed in late 2000 and late 2001 following dry season fires. Seedling density and height was assessed in late 2000 (after the dry season fires) and early in 2001 and 2002 (after the wet season but before dry season fires). The cover of all woody and semi-woody plant species, and ground layer and substrate components, was assessed early in the 2001 dry season prior to any fires. Two plots, one at each site, could not be re-located in 2002 because of rampant growth of seedlings and other herbage.

The density and height class of *B. arnhemica* seedlings was scored in a strip transect of variable width (10, 30 or 100 cm, depending on the initial seedling density) immediately up-slope from the secondary transect. Height classes were: 0–20 cm, 20–50 cm, 50–100 cm, 1–2 m, 2–5 m or > 5 m. All woody or semi-woody plant species in the plots were identified and scored for canopy cover in classes: 1 = <1%; 2 = 1–5%; 3 = 5–10%; 4 = 10–25%; 5 = 25–50%; 6 = 50–75%; 7 = 75–100%. For this analysis, the cover of bamboo was estimated from the presence of old (mostly dead) clumps, whose standing culms persisted for several years after flowering. Substrate, extent of fire, and ground-layer cover was assessed at 100 points arranged at 10 cm intervals along the secondary transect. Substrate classes were: *soil*, *gravel* (< 2 cm diameter) or *rock* in size classes of 2–5, 5–10, 10–25, 25–100 and > 100 cm diameter. Ground-layer classes were: bamboo seedlings, grass, forbs, litter and bare. "Grass" is defined to exclude *B. arnhemica*, whilst "herbage" is taken to include *B. arnhemica* seedlings, grass and forbs.

Shadehouse experiment

Three shadehouse trials were conducted in which the response of seedlings to removal of all above-ground parts with secateurs was examined and compared with control groups (Table 1). All seed was from a well-mixed sample collected from six wild stands on 6 Nov. 2000. After an initial period in seedling trays, vigorous seedlings were potted individually in 12 cm pots with 50% sand and 50% locopeat, kept under 30% shadecloth and watered twice daily. Within trials, plants were randomly allocated to treatment or control groups.

Table 1. Details of shadehouse experiments involving the removal of above-ground parts of *Bambusa arnhemica* seedlings.

Trial	Dates (no. of days after previous stage)			No. of plants		Parameters assessed
	Sowing	Trial start	Trial finish	Treatment	Control	
1	12 Nov. 2000	1 Feb. 2001 (81)	2 Apr. 2001 (61)	10	10	survival
2	12 Nov. 2000	20 Mar. 2001 (128)	25 May 2001 (66)	20	13	survival number of culms height of tallest culm diameter at base of largest culm
3	16 Dec. 2001	20 Mar. 2001 (94)	25 May 2001 (66)	15	18	survival number of culms height of tallest culm diameter at base of largest culm

Data analysis

Maps incorporating GPS field data and digital elevation data were prepared in ArcView GIS 3.2 (ESRI 1992-2000).

Daily average river depth data for the 40 years to 2002 was obtained from the managing agency (Department of Infrastructure, Planning & Environment) for the Dirty Lagoon gauge. The gauge does not operate consistently when water levels are below the high-tide mark, a condition characteristic of the dry season when non-tidal flows are miniscule. The dataset was screened for missing data not explicable as low water levels, uncertainties being clarified with agency staff. Years (defined as beginning on September 1 so as to embrace entire wet seasons) with incomplete data were excluded, reducing the sample to 27 years.

Ordinations and vector-fitting was performed in PC-ORD (McCune and Mefford 1999) using cover scores for woody and semi-woody plants present in at least three plots. Ordinations were Bray-Curtis using the Sorensen (Bray-Curtis) distance measure, the variance-regression method of endpoint selection and Euclidean axis projection. Vectors for continuous variables were fitted by Weighted Averaging. Two sets of vectors were fitted, the species used in the ordination, and a set of ground and rock cover variables - bamboo seedlings, grass, forbs, litter/bare ground, total rock, rock (2–10 cm), rock (10–100cm), rock (2–100cm), rock (>100 cm). A significance threshold for vector coefficients of determination was established using a Bonferroni correction to $P = 0.05$ for the number of variables in the set.

Bamboo seedlings have numerous culms arising from below the ground and often occurred at very high densities, so that density estimates were inevitably imprecise. Prior to analysis, densities were converted to an ordinal scale of: 0 = 0 seedlings, 1 = 0.1–0.4 m^{-2}, 2 = 0.4–1.0 m^{-2}, 3 = 1.1–4.0 m^{-2}, 4 = 4.1–10.0 m^{-2}, 5 = 10.1–40.0 m^{2} and 6 = > 40.1 m^{-2}. Effects on seedling densities (site, % burnt in 2000, cover of old clumps) were examined for plots with old bamboo clumps by generalized linear models using the ordinal multinomial distribution and log-log link function. Effects and their two-way interactions were removed by backward stepwise analysis until only effects significant at $P < 0.05$ remained.

Results

Vegetation and floristics

At Heathers Lagoon, riparian forest occupied a height of *c.* 4.5 m from the high-tide mark upwards to within 0.5 m of the somewhat irregular top of the levee, whilst savanna occupied the more or less level ground above. *Bambusa arnhemica* occurred through the height range of the riparian forest but at lower frequency close to the high-tide mark, where it was largely replaced by *Melaleuca leucadendra*, *Pandanus spiralis*, *Barringtonia acutangula* and *Nauclea orientalis*. Old clumps of *Bambusa arnhemica* occurred in all nine riparian plots, with cover class medians from 18 to 62%. It was mono-dominant in five plots, co-dominant with *Melaleuca leucadendra* (2 plots) or *Corymbia confertiflora* (1 plot) or sub-dominant to *Melaleuca leucadendra* (1 plot). The latter plot was the lowest-lying and the only one of the nine in which no *B. arnhemica* seedlings were found. Neither old clumps nor seedlings were found in the four savanna plots.

In the Bamboo Creek area, an extensive series of vine-thicket stands of *B. arnhemica* occurred on either or a combination of (*a*) steep, rocky slopes leeward of prevailing dry season winds, (*b*) on the leeward side of emergent bedrock bars, or (*c*) immediately upslope from perennially moist evergreen rainforest vegetation associated with springs and a perennial stream (Fig. 1), with a few old clumps and seedlings within but close to the margins of the evergreen rainforest. *Bambusa arnhemica* was present as old clumps in 17 of 26 plots with cover class medians from one to 62%, and as seedlings in 15 plots all of which also had old clumps.

Eighty-three species of woody or semi-woody plants were recorded in the 39 plots, 22 species at Heathers Lagoon and 72 at Bamboo Creek. The large difference reflected not only the greater number of plots at Bamboo Creek, but also the greater diversity of habitats, the outstanding species-richness of both the evergreen rainforest and the rocky-slope vine-thicket, and also the diversity of the woody-plant understorey in the rocky slope savanna. Of the eleven species that occurred at both sites, only two, *B. arnhemica* and *Acacia auriculiformis*, occurred in more than two plots at each site, indicating marked floristic dissimilarity between the sites. *Acacia auriculiformis* was mainly associated with riparian vegetation at Heathers Lagoon and the evergreen rainforest at Bamboo Creek (Table 2).

Table 2. Plant species occurring in more than 50% of plots in any of the habitats defined *a priori* (Fig. 3).

For the Bamboo Creek site, ERF = evergreen rainforest; Adj. = two non-rocky plots on the flat adjacent to the rainforest; RSlope = rocky slope.

Species	Frequency				
	Heathers Lagoon		Bamboo Creek		
	Riparian	Savanna	ERF	Adj.	RSlope
n	9	4	4	2	20
Bambusa arnhemica	9	0	3	0	14
Phyllanthus reticulatus	7	0	0	0	0
Barringtonia acutangula	6	0	0	0	0
Melaleuca leucadendra	6	0	0	0	0
Acacia auriculiformis	6	1	2	1	0
Antidesma ghesaembilla	3	3	0	0	1
Corymbia confertiflora	2	4	0	0	0
Planchonia careya	0	4	0	1	0
Eucalyptus bigalerita	0	4	0	0	0
Syzygium nervosum	0	0	4	0	0
Carpentaria acuminata	0	0	3	0	0
Horsfieldia australianum	0	0	3	0	0
Terminalia microcarpa	0	0	3	1	0
Corymbia bella	1	1	0	2	0
Canarium australianum	0	0	0	1	13
Corymbia polysciada	0	0	0	0	13
Erythrophleum chlorostachys	0	0	0	1	16

A three-dimensional ordination of all plots yielded aggregations consistent with *a priori* habitat groupings, but only the Heathers Lagoon savanna (Fig. 3) and the Bamboo Creek evergreen rainforest (along the third axis, not shown) formed discrete groups in ordination space. A floristic continuum of all plots with *B. arnhemica* from riparian through evergreen rainforest to rocky vine-thicket is evident on the first two axes, as also are continua between many plots with and without *B. arnhemica*. Plants associated with *a priori* groups are listed in Table 2.

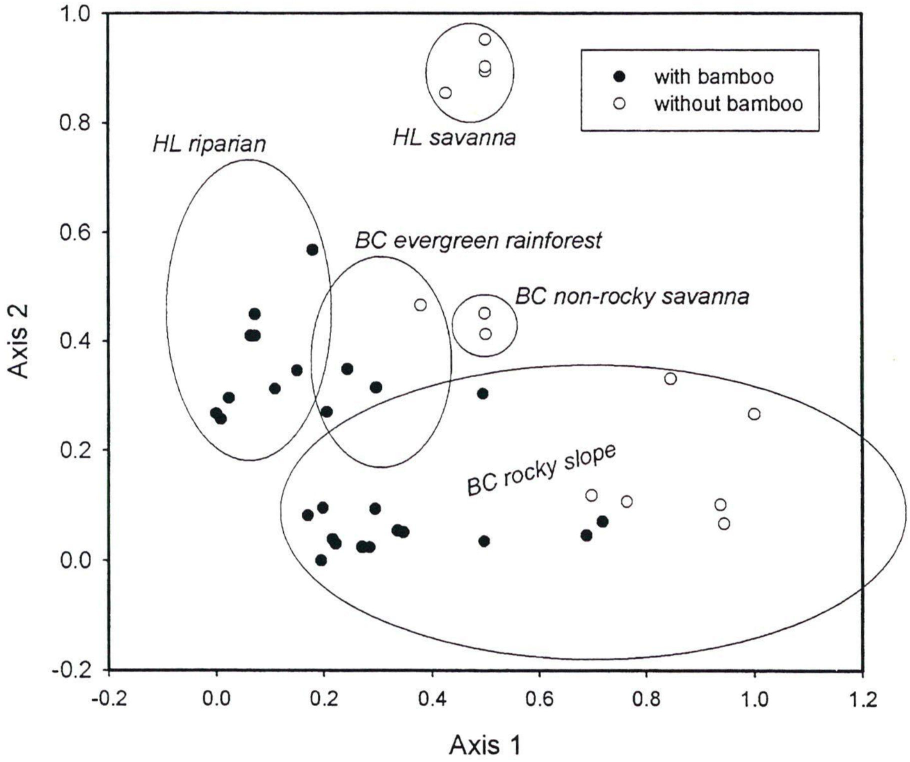

Figure 3. The first two axes of an ordination of all plots by cover scores of the 47 woody and semi-woody plants present in at least 3 plots.

Ellipses enclose habitats defined *a priori*. HL = Heathers Lagoon, BC = Bamboo Creek. The first two axes of the ordination accounted for 44% of the variance, the third axis (not shown) an additional 15%.

The first two axes of a three-dimensional ordination of Bamboo Creek rocky slope plots and associated vector-fitting identified two floristic gradients, one from *B. arnhemica* vine-thicket to *Eucalyptus miniata* savanna and the other from the trees *Corymbia polysciada* to *Erythrophleum chlorostachys*. The former was not or scarcely related to rockiness, whereas the latter was strongly so (Fig. 4*b*).

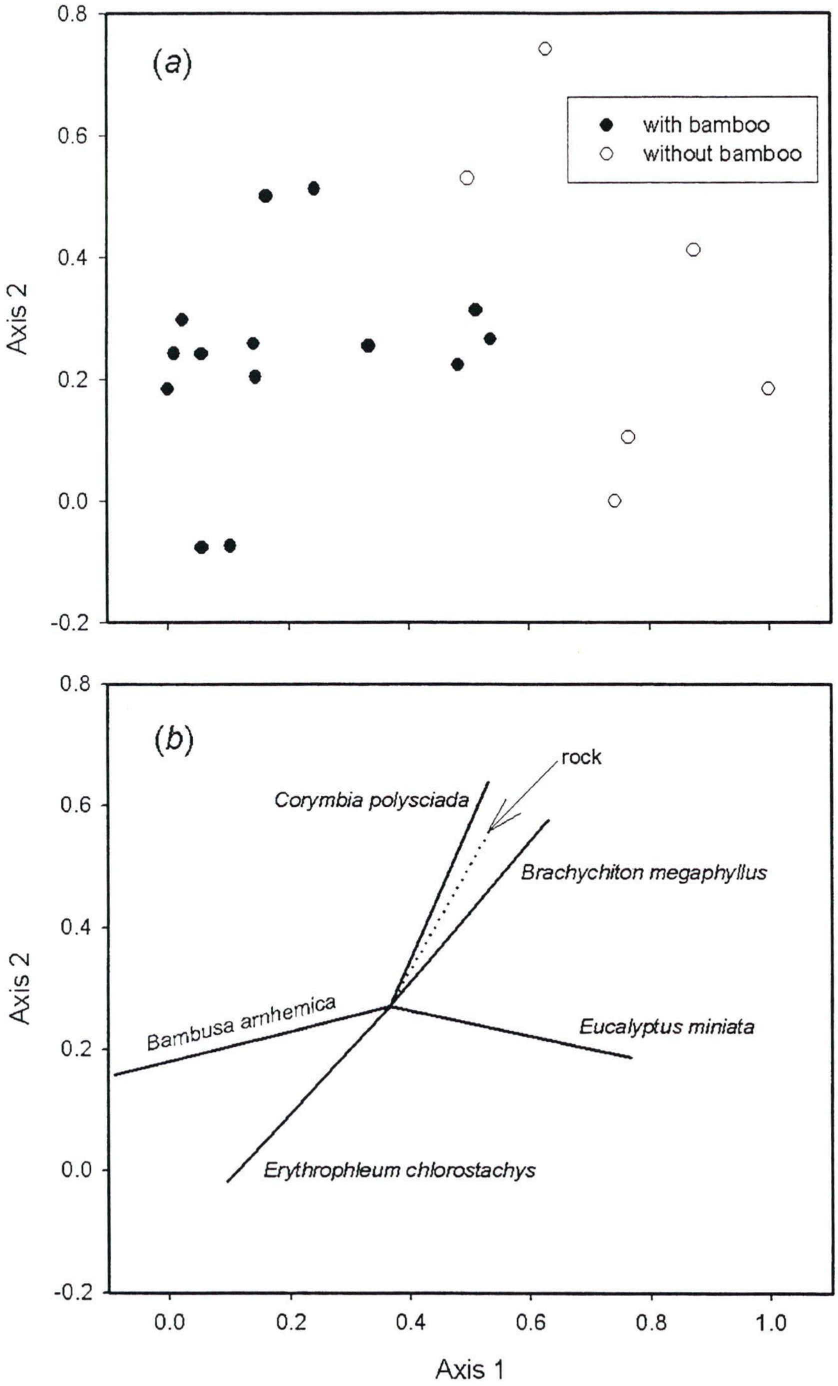

Figure 4. ***a.*** **The first two axes of an ordination of Bamboo Creek rocky slope plots by cover scores of the 24 woody and semi-woody plants present in at least 3 plots. The first two axes accounted for 65% of the variance, the third axis (not shown) an additional 12%.** ***b.*** **Significant vectors (*P* < 0.05, Bonferroni-corrected) for species (solid lines) and rock and groundcover attributes (dotted lines).**

Three rock variables (total rock, rock 2–10 cm, and rock 2–100 cm) were significant but were fairly strongly aligned and are for graphic simplicity represented here by the vector for total rock alone. The length of the vector indicates the relative strength of the correlation.

Flooding and soil moisture

Approximately half the riparian forest at Heathers Lagoon was subject to annual inundation by floodwaters, whilst the upper edge of the riparian forest and the adjacent savanna were inundated in *c.* 75% of years (Table 3). At their extreme downslope position, *B. arnhemica* clumps were inundated annually for an average of *c.* 60 days including 40 consecutive days, the corresponding figures for their upslope extreme being *c.* 14 and 8 days. Gauge data for the wet season following the germination of seedlings (1999/2000) are incomplete, with almost all January data missing. The available data shows that the entire bamboo stand was inundated for at least 30 days including 23 consecutive days, and seedlings at 6.0 m gauge height for at least 71 days including 49 consecutive days. Brief and incomplete flooding of seedlings occurred in November and December, but the major flood event took place in February and March. The adjacent savanna was inundated for at least 24 days. Data are missing for substantial key periods of the 2000/01 wet season, but the entire stand of riparian vegetation and the adjacent savanna was again inundated, with a recorded flood peak of 11.2 m.

At Bamboo Creek, only the evergreen rainforest plots were subject to wet-season flooding, these being moist to swampy throughout the dry season as well, with springs evident in a number of places. There was no evidence of springs or other supplementary moisture in any other plot.

Surface rock

There was no surface rock at Heathers Lagoon, and little or no surface rock (range 0–2%) in the evergreen rainforest plots or two plots in the adjacent savanna on level ground at Bamboo Creek. The remaining plots at Bamboo Creek (n = 20), all on moderate to steep slopes, had rock cover of 23–86% comprising boulder screes (modal rock size class 10–25 cm, Table 4) loosely or not embedded in soil. Occasional emergent bedrock was a secondary feature found only on the mid- and upper-slope plots. There was no significant differences between plots with and without old clumps of *B. arnhemica* in the cover of any rock size class (Table 4), the lack of significant difference being maintained when the two plots with low cover of old clumps of *B. arnhemica* (cover classes 1–2, *cf* 4–6 in the remaining plots) were included with those that had none.

Table 3. Extent of inundation of the river bank at the Heathers Lagoon site as indicated by the nearby Dirty Lagoon gauge, Adelaide River, 1962–63 to 2001–02.

n = 27 years for which there are complete data. Years are from Sept. 1 to August 31 so as to embrace entire wet seasons within a "year". Source data are daily average depths. Zero gauge height is an arbitrary starting point possibly relating to the river bed.

Gauge height (m)	% of years reached	Days/year under water		Max. consecut. days/year under water	
		Median	Range	Median	Range
13.0	11	0	0 – 2	0	0 – 2
12.0	22	0	0 – 4	0	0 – 4
11.0	59	3	0 – 17	3	0 – 12
10.0	70	6	0 – 38	5	0 – 20
9.0–9.5	**top of levee**				
9.0	78	14	0 – 45	8	0 – 25
8.5	**uppermost level of *Bambusa arnhemica***				
8.0	85	20	0 – 58	12	0 – 39
7.0	100	27	2 – 69	15	1 – 55
6.0	100	36	4 – 89	26	4 – 83
5.0	100	56	13 – 100	37	7 – 97
4.3	**high tide mark**				

Table 4. Rock profile of plots with (*n* = 14) and without (*n* = 6) old clumps of *B. arnhemica* on the rocky slope at Bamboo Creek.

Comparisons of habitat medians are non-parametric: n.s. = not significant (*P* > 0.05).

Rock class	%cover (median, range)		Difference
	bamboo	no bamboo	
rock 2 – 5 cm	5.5 2–15	4 1–9	n.s.
rock 5 – 10 cm	9 3–33	12.5 6–24	n.s.
rock 10 – 25 cm	18 8–32	17 10–45	n.s.
rock 25 – 100 cm	9.5 0–19	10.5 1–23	n.s.
rock > 100 cm	0 0–22	4 0–29	n.s.
total rock	49 23–84	65 33–86	n.s.

Groundcover

Prior to being burnt, the savanna plots at Heathers Lagoon carried a dense sward of 0.5 – 1.0 m tall perennial grasses, whereas the riparian plots had a variable cover of mostly low (< 0.3 m) annual or perennial grasses, and *B. arnhemica* seedlings (Table 5). At Bamboo Creek, grass and herbage cover was highest in the non-rocky savanna and least in the evergreen rainforest, the converse being true for bare ground/litter, but the rocky slope was highly variable for these parameters with an intermediate median (Table 5). A correlation matrix of seedlings, grass, forb and bare ground/litter cover for the 20 rocky slope plots yielded only one significant relationship, a negative correlation between grass and bare ground/litter cover ($r_s = -0.61$, $P = 0.005$).

Table 5. Groundcover attributes of plots at Heathers Lagoon and Bamboo Creek prior to the 2001 dry season fires.

Seedlings are *Bambusa arnhemica* seedlings. Comparisons of habitat medians within sites are non-parametric: n.s. = not significant, * = $P < 0.05$, ** = $P < 0.01$. Medians for bare-litter are reciprocal to those of herbage, and thus statistical comparisons are identical.

Site/habitat	*n*	Cover % (median, range)				
		seedlings	grass	forbs	herbage	bare/litter
Heathers Lagoon						
riparian	9	29 0–93	0 0–54	3 0–46	68 27–93	32 7–73
savanna	4	0 0	85 79–94	1 0–4	85 83–96	15 4–17
comparison		*	**	n.s.	n.s.	n.s.
Bamboo Creek						
evergreen rainforest	4	1 0–5	0 0–3	7 1–14	11 3-14	89 86–97
non-rocky savanna	2	0 0	80 75–85	4 0–8	84 83–85	16 15–17
rocky slope	20	2 0–69	26.5 1–86	9 0–19	58 6–91	42 9–94
comparison		n.s.	**	n.s.	**	**

Fire

At Heathers Lagoon, late-season fires burnt all savanna plots in both years, but scarcely penetrated the riparian forest, burning only one or two up-slope, and no down-slope riparian plots (Table 6). At Bamboo Creek, fires appear to have been deliberately lit in both years, burning upslope from a series of ignition points close to the edge of the evergreen rainforest. Fire scarcely penetrated the evergreen rainforest, but burnt at least part of most other plots in both years (Table 6). However, there was a significant difference between years in the cover of the burns in the rocky slope plots (Wilcoxon test, *P* = 0.005). The 2000 fire was the more extensive, burning all of 18 rocky slope plots and 79% of another, leaving just one unburnt. In contrast, the 2001 fire tended to burn around *B. arnhemica* stands, there being a strong negative correlation between the cover of seedlings and the percentage burnt ($r_s = -0.82$, n = 20, *P* = 0.00001).

Numerous dead standing and fallen culms from the previous generation of *B. arnhemica* persisted throughout the study period even in plots that were burnt.

Table 6. Timing and extent of fire in plots at Heathers Lagoon and Bamboo Creek. "No. of plots" burnt includes part-burnt plots. Comparisons of habitat medians are non-parametric: n.s. = not significant, * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001. Medians for bare-litter are reciprocal to those of herbage; thus statistical comparisons are identical.

Site/habitat	*n*	burnt (no. plots, %burnt median, %burnt range)					
		2000			2001		
Heathers Lagoon							
timing		Aug. or Sept.			late July or early Aug.		
riparian	9	1	0	0–100	2	0	0–60
savanna	4	4	100	39–100	4	100	70–100
comparison			*				**
Bamboo Creek							
timing		unknown			mid-June		
evergreen rainforest	4	1	0	0–1	0	0	0
non-rocky savanna	2	2	100	100	2	53.5	7–100
rocky slope	20	19	100	0–100	18	86	0–100
comparison			***				n.s.[A]

[A] *P* = 0.054

Seedling survival and growth in the field

Seedlings of *B. arnhemica* occurred in eight of nine plots at Heathers Lagoons that had old clumps of *B. arnhemica*, and in 16 of 17 such plots at Bamboo Creek, but in no plots that lacked old clumps. All subsequent analysis in this section is restricted to plots with old clumps.

Median (maximum) density estimates (where available, see *Methods*) were 10.3 (141) m^{-2} in 2000, 3.4 (64) m^{-2} in 2001 and 2.0 (24) m^{-2} in 2002. In 2002, seedlings remained present in 23 of 26 plots, with density estimates of more than 1.0 m^{-2} for 15 plots and more than 10 m^{-2} for six. The correlation between seedling density in 2001 (the year for which the most comprehensive set of data is available) and the cover class of old clumps (Fig. 5) was significant and positive at Bamboo Creek (r_s = 0.85, n = 17, *P* = 0.00002), but not at Heathers Lagoon (r_s = 0.54, n = 9, *P* = 0.13). The seedling population gained height during the study period, reaching a median and modal height class of 1–2 m, and a maximum height of more than 5 m, after three wet seasons (Fig. 6).

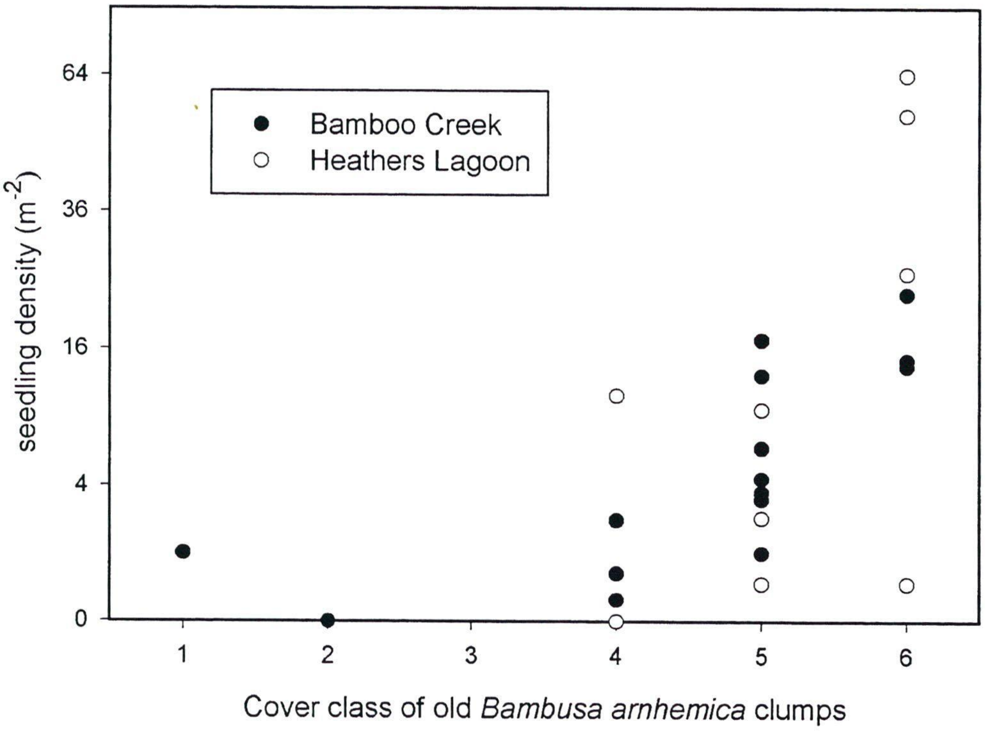

Figure 5. Density of *Bambusa arnhemica* seedlings in the early dry season of 2001 - *c.* 18 months after germination - as a function of the cover of old *B. arnhemica*. clumps. See Methods for details of the cover classes.

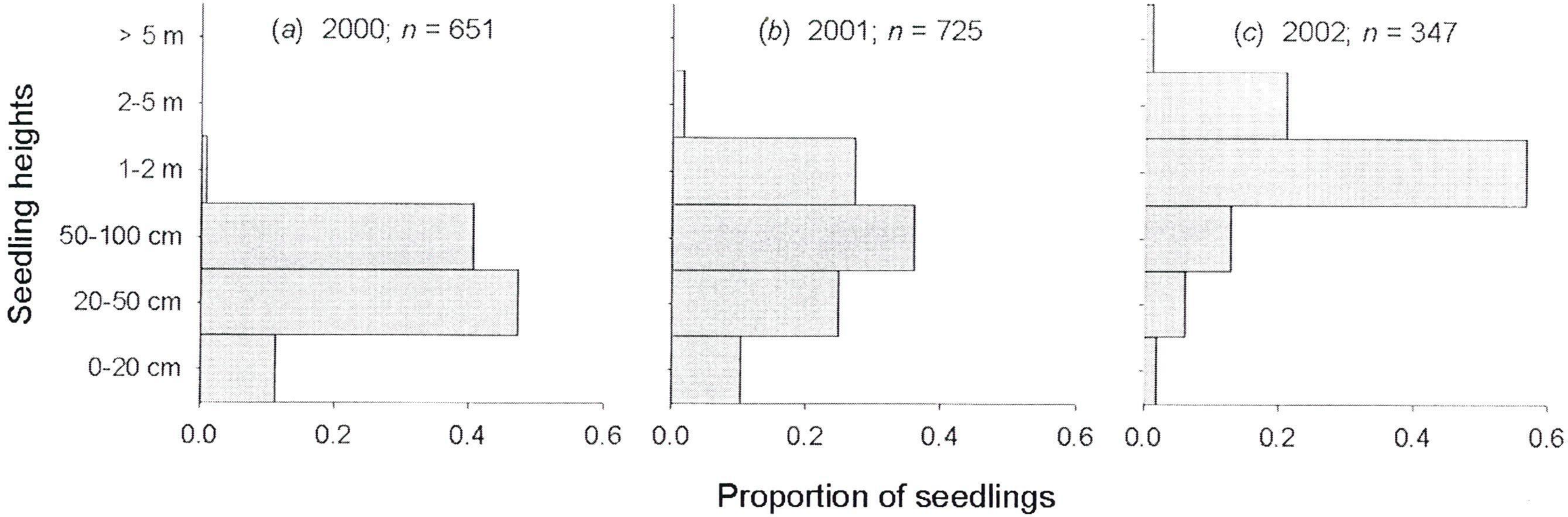

Figure 6. Height profiles of *Bambusa arnhemica* seedlings from all available plots over three years.

The 2000 data were collected later in the year and from the limited number of plots that were unburnt, or unburnt seedlings in partly burnt plots.

When burnt, all above-ground parts of the seedlings were usually killed and consumed, leaving culm stubs to *c.* 1 cm as the only evidence of their presence. Regeneration occurred by the production of new culms from underground rhizomes (Fig. 7). Neither fire (%burnt in 2000) nor site was a significant effect on the density of seedlings in 2001, stepdown linear modelling excluding these variables and all two-way interactions, leaving the cover class of old bamboo clumps as the sole significant effect ($n = 26$, Wald's Chi-square = 7.7, d.f. = 1, $P = 0.005$). After a wet season of regeneration, there was no significant difference in seedling heights between plots at both sites that were 100% burnt in 2000 and those not burnt (Table 7). After two wet seasons of regeneration, seedlings in plots 100% burnt in 2000 had a median of plot median heights of 1–2 m and tallest heights of 2–5m. No plot with more than 1.0 seedlings m^{-2} was 100% burnt in both years; those in two rocky slope plots burnt 100% in one year and more than 60% in the other both achieved median and modal seedling height classes of 1–2 m and maximum height classes of 2–5 m. Seedlings in the evergreen rainforest plots at Bamboo Creek, which were never burnt, achieved a modal height class of 50–100 cm and a maximum height class of 1–2 m in 2002, considerably less than the equivalent values overall (Fig. 6).

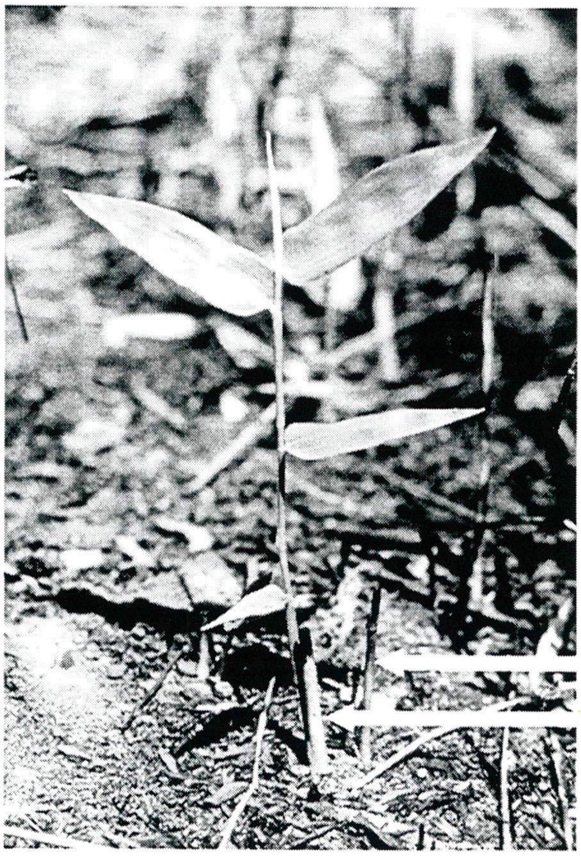

Figure 7. New culm of a Top End Bamboo (*Bambusa arnhemica*) seedling produced after fire. Arrows indicate the stubs of burnt culms.

Table 7. Heights of bamboo seedlings after the 2000–01 wet season in plots burnt and not burnt in the 2000 dry season.

Height classes: 2 = 20–50 cm; 3 = 50–100 cm; 4 = 1–2 m; 5 = 2–5 m. Most 100% burnt plots were at Bamboo Creek and most unburnt plots at Heathers Lagoon.

Burn state	median	range	*n*	*U*	*P*
Plot median heights					
100% burnt	2.5	2–3	9		
unburnt	3	2–4	7	17	0.14
Plot tallest heights					
100% burnt	4	3–5	9		
unburnt	4	4–5	7	24.5	0.47

Seedling survival and growth in the shadehouse

Forty percent of seedlings treated by the removal of all above-ground parts 81 days after being sown survived, whereas 73% of those treated at 94 days and 95% of those treated at 128 days survived. All control seedlings survived.

Qualitatively, the control groups of shadehouse seedlings grew as well as the most vigorous wild seedlings, suggesting that shadehouse conditions were favourable. There were significant negative effects of removal of all above-ground parts on number of culms, maximum height and maximum culm diameter in both Trials 2 and 3 (Table 8). However, there was overlap between control and treatment groups in the range of responses for all except height in Trial 2. There were no significant differences between removal groups 2 and 3 for any response variable.

Table 8. Response of surviving seedlings to experimental removal of all above-ground parts.

The parameters of each response are the mean, standard deviation and range. As variances are proportional to means, data were square-root transformed for the purpose of comparisons between treatment and control groups using *t*-tests. n.s. = not significant ($P > 0.05$); ** = $P < 0.01$; *** = $P < 0.001$.

Trial	Treatment	*n*	No. of culms	Height (cm)	Diameter (mm)
2	removal	19	3.3 ± 2.28	20.6 ± 6.74	1.71 ± 0.513
			1–10	4–30	0.8–3.0
	control	13	8.6 ± 3.88	61.1 ± 10.05	3.32 ± 0.867
			5–15	41–75	1.7–4.4
	comparison		***	***	***
3	removal	11	4.2 ± 2.09	16.4 ± 6.28	1.40 ± 0.520
			2–8	8–30	0.7–2.3
	control	18	7.3 ± 3.43	39.0 ± 8.98	2.61 ± 0.640
			5–17	21–51	1.7–3.6
	comparison		**	***	***
Comparison of removal groups			n.s.	n.s.	n.s.

Discussion

Seedlings, fire and flood

Seedling populations of *B. arnhemica* were remarkably tolerant of inundation for at least 70 days during their first wet season, or of the loss of all above-ground parts to fire in their first dry season, subsequently growing vigorously. However, prolonged inundation and/or flood scouring might have been responsible for the absence of seedlings from the most low-lying plot at Heathers Lagoon. Two-and-a-half years after germination and regardless of disturbance, the density of seedlings exceeded the density of old clumps by up to two orders of magnitude in most bamboo plots, mature clump density being less than 0.1 m^{-2} in even the most dense monodominant stands (Franklin unpubl. data).

Although the age of seedlings burnt in 2000 can only be estimated, it is likely to have been between 180 and 320 days, germination in *B. arnhemica* being triggered promptly by the first substantial rains of the wet season, typically in October or November (Franklin pers. obs.). The experimental removal of above-ground parts in shadehouse plants indicates enhanced survival capability with age, with only limited mortality amongst seedlings more than 120 days old, an age that ensures enhanced survival capability before the onset of the first dry season. Similarly, Banik (1990) reported near complete mortality of wild bamboo (*Bambusa tulda* and *Dendrocalamus longisphathus*) seedlings burnt before three months of age, but vigorous regeneration after burning with complete loss of above-ground parts at six to nine months. The ability of bamboo seedlings to survive fire is thought to relate to the development of rhizomes (Keeley and Bond 1999). In most bamboo species, development of secondary culms is by tillering, rhizome development commencing only after "several" such secondary culms have been produced by the seedling (McClure 1966; Judziewicz *et al.* 1999). It is unclear whether these age-enhanced survival capabilities are also relevant to flood tolerance, but a flood peak in February and March may have been sufficiently delayed to permit rhizome development.

Even though fires burnt up to the fringe of seedling stands at both sites in both years, most plots at Heathers Lagoon containing *B. arnhemica* seedlings were not burnt in either year, and most of those at Bamboo Creek were not burnt in 2001. *Bambusa arnhemica* seedlings may therefore be somewhat fire retardant. They remain green for much longer into the dry season (unpubl. data) than most native annual and perennial savanna grasses of northern Australia (Williams *et al.* 1998).

Notwithstanding their tolerance of fire and flood, neither source of disturbance was essential for the germination or survival of *B. arnhemica* seedlings. Dense and vigorous seedling growth was observed to occur in the one plot (at Bamboo Creek) and extensive nearby areas that were neither burnt nor flooded in the two-and-a-half years following flowering, die-off and germination. However, seedlings grew poorly on the fringe of the evergreen rainforest and were absent within it, one of several possible explanations for which being that there was insufficient light.

Bamboo in the landscape

The Heathers Lagoon and Bamboo Creek study sites differed markedly in floristics, parent material, soil structure, drainage and surface rock characteristics, demonstrating broad ecological tolerance on the part of *B. arnhemica*. This versatility, along with the patchy distribution of *B. arnhemica* at Bamboo Creek and its absence from the adjacent savanna landscapes, begs explanation. The possibility that riparian and rocky vine-thicket bamboo stands attributed to *B. arnhemica* might be cryptic distinct species has been ruled out by a combination of detailed morphological examination (Franklin ms) and genetic (AFLP) analysis of 27 polymorphic bands (Isagi, Tsukagoshi and Franklin unpubl. data).

At the Heathers Lagoon site and on non-rocky ground at Bamboo Creek, the occurrence of *B. arnhemica* was sharply and negatively related to the occurrence of eucalypts and other perennial grasses - the savanna. The pattern was less clear on the rocky slope at Bamboo Creek where vegetation varied markedly in a fine-scale mosaic, but a negative relationship between *B. arnhemica* and the dominant eucalypts *Corymbia polysciada* and *Eucalyptus miniata* is evident (Fig. 4). It seems likely, though unconfirmed, that the soils at both Heathers Lagoon and Bamboo Creek are more fertile than the impoverished lateritic soils characteristic of much of the adjacent savannas (Mott *et al.* 1985). However, discontinuities in soil fertility appear unable to explain the distribution of *B. arnhemica* within the sites including its absence from savanna plots, both sites having strikingly uniform soils throughout. This study also failed to identify localised edaphic discontinuities such as rockiness or flood limits that could account for the often sharp boundaries to *B. arnhemica* stands.

More evidence is needed to determine the processes limiting the occurrence of *B. arnhemica* at the patch and landscape scale. Several possibilities appear worthy of further investigation. Seed dispersal may be severely limited, as the seed is a large caryopsis (mean air-dry weight 19.3 mg) with no awns or other apparent dispersal mechanism (Franklin ms). The apparent incongruity of the tolerance in *Bambusa arnhemica* to a single fire combined with its limitation to somewhat fire-protected sites is characteristic of many Australian rainforest plants (Bowman 2000, 2001). Liddle *et al.* (1994) and Booth *et al.* (2001) treated *B. arnhemica* as a rainforest species, a classification perhaps reflecting its "not savanna" occurrence. The niche of *B. arnhemica* may be related to the openness of canopy needed for regeneration and associated with rainforest fringes, repeated disturbance by flooding or the semi-deciduousness of drier non-savanna sites, along with avoidance of sites subjected to recurrent fires. The tall-grass savannas and extensive floodplains that frame the distribution of *B. arnhemica* have a long history of high fire frequencies associated with both current (e.g. Press 1988; Gill *et al.* 2000), and pre-European (Russell-Smith *et al.* 1997; Preece 2002) management regimes. At Bamboo Creek, *B. arnhemica* vine-thickets occurred in topographically *relatively* fire-protected locations (Fig. 1). The position of the riparian forest at Heathers Lagoon on the river bank upslope from permanent water and downslope from the adjacent savanna also provides a degree of topographic fire protection. At the plot scale, the distribution of fine fuels (excluding *B. arnhemica* seedlings) is doubtless important. The riparian forest at Heathers Lagoon had markedly lower fine fuel levels than the adjacent savanna. The strong tendency of fire to burn around stands of seedlings at Bamboo Creek in the 2001 dry season also suggests such an effect.

We propose, therefore, that *B. arnhemica* is a fire-refugial species, tolerant of occasional fire but unable to persist in the face of frequent fires, its capacity to regenerate repeatedly from rhizomes restrained by soil fertility and/or moisture. Feedback mechanisms involving the suppression of fine grass fuels (Bowman and Wilson 1988) and possibly nutrient cycling (Bowman 1992) may enhance patchiness derived from subtle environmental gradients (Wilson and Nisbet 1997). Rocks may provide protection for seedling rhizomes from sterilisation of sub-surface soil by even the most intense of fires.

The bamboo fire-cycle hypothesis

The remarkable phenomenon of gregarious semelparity in long-lived bamboos is poorly documented and explanations for it largely speculative. The fire-cycle hypothesis (Keeley and Bond 1999) is requisite on several features of bamboo biology including: *a.* either seed or seedlings must have the ability to cope with fire; and *b.* either or both dead clumps and/or seedlings must be readily flammable and thus fire-promoting. For *B. arnhemica*, we found evidence for the former proposition, but interpret our findings as contrary to the second. Like most bamboos of the monsoonal tropics (Dransfield and Widjaja 1995; Keeley and Bond 1999), prompt germination of seed after flowering means that it is seedlings rather than seed which are exposed to wildfire; *B. arnhemica* seedlings coped well with being severely burnt at least once. However, whilst seedlings will burn in some circumstances, in one of two years at Bamboo Creek and both years at Heathers Lagoon fires burnt to the edge of but not or scarcely into seedling stands. Furthermore, many dead bamboo culms from the previous generation remained untouched even where fire had removed all seedlings and other herbage. It is our strong impression that both the seedlings and dead culms of *B. arnhemica* are fire-retardant rather than fire promoting, a conclusion consistent with evidence of a fire-refugial distribution and with the observation that culms of *Bambusa polymorpha* in Burma do not burn readily for a number of years after death (Ne Win 1951).

The generality that bamboo seedlings are light demanding (Tewari 1992; but see Taylor and Qin Zisheng 1988 and Stern *et al.* 1999 for possible exceptions in high-altitude forests) appears to hold for *B. arnhemica*. Death of parents in unburnt monodominant stands and open forests and semi-deciduous vine-thickets where there is a significant component of *B. arnhemica* appears to create sufficient light to sustain vigorous seedling growth. Even with fire, we found seedlings only in plots which also had old clumps, and the density of seedlings was positively related to the extent of old clumps. It is plausible that the fire-cycle hypothesis might apply where bamboo occurs in extensive patches within closed-canopy forests (e.g. Nelson 1994), but it appears inapplicable in landscapes subject to high fire frequencies such as in this study or where bamboos occur in scattered smaller stands (Gadgil and Prasad 1984). The suggestion (Gadgil and Prasad 1984; Campbell 1985) that parental death serves to provide sufficient canopy opening for seedling growth without invoking fire-cycles is a more parsimonious and universal explanation for the evolution of semelparity in bamboos.

Janzen (1976) briefly considered but rejected the notion that parental death is an adaptation to make way for seedlings because the hypothesis suffers from the "group selection" problem (Wilson 1987). Keeley and Bond's (1999) fire-cycle hypothesis is also potentially group selectionist. Gadgil and Prasad (1984), Wilson (1987, 1997) and Keeley and Bond (1999) proposed that kin selection could operate if dispersal distances were very small, as our data suggest, ensuring that parents died to make way for their own offspring or close relatives. Gregariousness need not be related to the provision of light gaps, as selective forces such as the benefits of seed-predator satiation (Janzen 1976; Curran and Webb 2000; Shibata *et al.* 2002) and improved pollination rates (Kelly *et al.* 2001; Satake and Iwasa 2002; Koenig and Ashley 2003) may also be operative. To move questions about the evolution of gregarious semelparity in long-lived organisms beyond speculation, research into seed and pollen dispersal distances and/or the intergenerational spatial genetics of relatedness is prerequisite and should be a high priority in the event of further mass-flowering in *B. arnhemica* or other gregarious-flowering, semelparous bamboos.

Acknowledgments

This project was funded by the Parks & Wildlife Service of the Northern Territory and the Key Centre for Tropical Wildlife Management. For their assistance under trying conditions in the field, we are grateful to Julian Gorman, Philip McMahon, Carmen Verhagen, Tim Davey, Gemma Cullen, Simon Tapley and Sarah Ghassemi. Staff of the Department of Infrastructure, Planning & Environment kindly provided river gauge and digital elevation data. Phil Ferenczi and Nigel Doyle of the Department of Mines & Energy provided geological advice. Quan Tien set up the shadehouse watering system. Peter Whitehead commented most helpfully on a draft of this manuscript.

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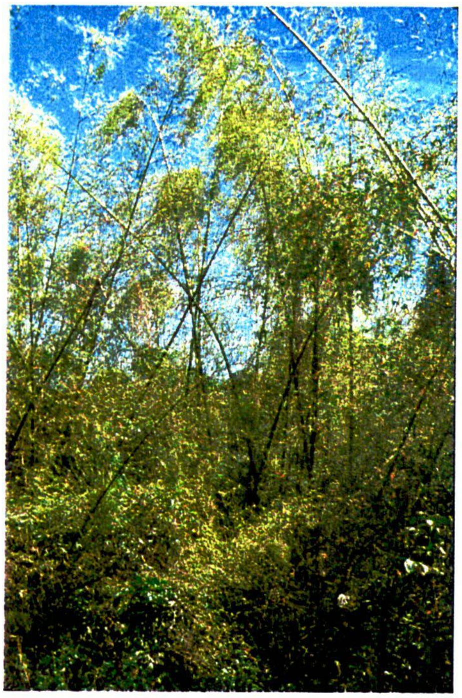
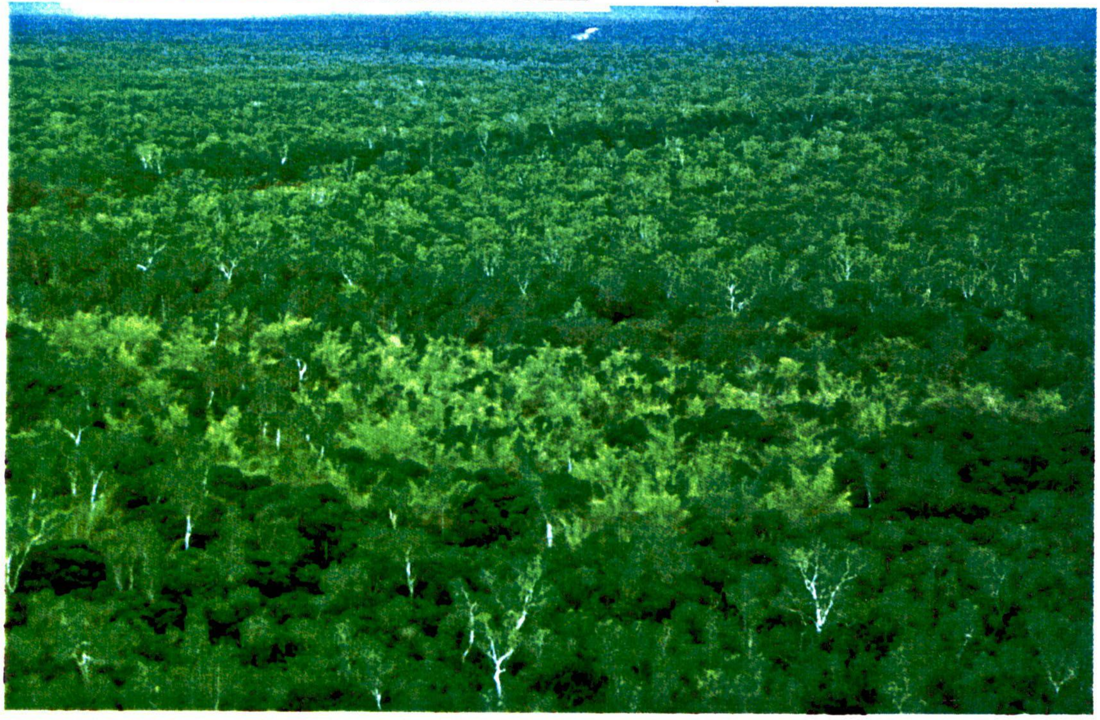
Chapter 5:

Flowering patterns

This chapter has been accepted for publication as:

Franklin DC. in press. Synchrony and asynchrony: observations and hypotheses for the flowering wave in a long-lived semelparous bamboo. *Journal of Biogeography*.





Abstract

Aim

(1) To describe the spatio-temporal patterns of mass-flowering and die-off in a long-lived, semelparous, clumping bamboo, *Bambusa arnhemica*, at landscape and local scales. (2) To discuss causal processes in the flowering patterns of semelparous bamboos.

Location

The entire range of *B. arnhemica*, in the monsoonal, tropical, north-west of the Northern Territory of Australia, mostly along watercourses.

Methods

Landscape-scale flowering patterns were assessed by a combination of air, boat and ground survey in each year from 2000 to 2002. Areas that flowered prior to 2000, and those in which no flowering occurred, were also recorded, and historic records collated. At local scales, initiation of flowering, rates of die-off, and subsequent germination densities of seedlings were quantified by ground-based counts.

Results

After an estimated 40–50 years of vegetative development, *B. arnhemica* flowered, seeded prolifically, then died. Flowering occurred synchronously within patches ranging from 0.002 to 3200 km^2. One or more patches flowered in successive years from 1996 to 2002, forming a temporally-structured but spatially-chaotic flowering wave that affected *c.* 80% of the population. Synchronous flowering took the form of a flowering distribution in which over 95% of clumps within a patch initiated flowering in a central year, most of the remainder flowering the year before or after. Along the Daly River, an exception was observed in which 56% of clumps flowered in the peak year. Seedling densities were three orders of magnitude greater under clumps that flowered in the central rather than the leading year of the flowering distribution.

Main conclusions

Synchrony is argued to be the primal state in semelparous bamboos, promoted by intense selection acting on a endogenous (genetic or biological) clock whose influence largely overrides that of the environment. A flowering wave may develop within an initially synchronous population when stochastic events interact with the biological clock without permanently altering the clock setting, producing an off-set patch. Off-set groups may only survive if sufficient individuals are off-set by the same amount at the same time and in the same vicinity so as to produce a new synchronously-flowering patch. This could be driven by two processes. Inter-year climatic variation may alter the biological clock's perception of time, producing off-sets at local or regional scales or even affecting entire populations. Severe environmental pressures may also force one-off changes to flowering schedules, as suggested by a severe flood event prior to flowering on the Daly River. A dynamic hypothesis for a wider range of bamboo flowering patterns is proposed in which synchronous flowering is fragmented and disrupted over time but renewed by allochronic speciation and dispersal.

Introduction

Many bamboos (Poaceae: Bambuseae) remain in a vegetative state for between thirty and sixty years, and several species for more than 100 years, before engaging in a suicidal bout of sexual reproduction (Janzen, 1976). Even more remarkably, the onset of flowering may be synchronous among ramets, genets and stands at a range of spatial scales. In India, Gadgil & Prasad (1984) documented synchronous flowering of bamboo stands in areas of up to 1,400 km^2, and areas of similar extent have been documented in temperate South America (Jaksic & Lima, 2003). In the Brazilian Amazon, synchronous flowering occurred in *c.* 10,000 km^2 of continuous mono-dominant bamboo forest (Nelson, 1994). Gregarious semelparity at large scales may have marked consequences for vegetation dynamics (Taylor & Qin Zisheng, 1992; Abe *et al.*, 2001; Gonzalez *et al.*, 2002) and bamboo-associated fauna (Taylor & Qin Zisheng, 1997; Carter *et al.*, 1999; Jaksic & Lima, 2003). It adversely affects the livelihoods of people dependant on bamboo resources (Rao & Rao, 1995; INBAR, 2003), and can trigger serious famine for subsistence farmers in the vicinity (Mohan Ram & Hari Gopal, 1981; Sajal Nag, 1999).

The dramatic nature of the phenomenon belies its complexity. From a largely anecdotal and often confused and confusing literature, of which the early account of Brandis (1899) and the review of Blatter (1929-30) are perhaps the most lucid, three and possibly four spatio-temporal patterns of flowering may be discerned amongst semelparous bamboos. The first, in which a small percentage of clumps flower the year (or two) before and after the main flowering, was termed the "flowering distribution" by Janzen (1976). The second, in which gregarious flowering occurs in patches in successive years has been described as a "flowering wave", apparently following Troup (1921). The third involves variations in periodicity between populations (e.g. Gadgil & Prasad, 1984; Banik, 1998) leading to diffuse temporality within a species. A possible fourth pattern, "sporadic flowering", may imply random or other non-gregarious patterns of flowering, but application of the term has been variable and ill-defined, and there is no convincing evidence that any semelparous bamboo has a reproductive strategy that may be regarded as "not gregarious" (see Gadgil & Prasad, 1984 for a contrary view). Most if not all semelparous bamboo species exhibit at least two of these variants, and some perhaps all four (e.g. Banik, 1998).

This complexity of patterns has prompted much discussion about the cues for the initiation of flowering. A more or less fixed, species-specific periodicity to the phenomenon has been described over at least two generations in a few species (Kawamura, 1927; Janzen, 1976; Bahadur, 1980; Mohan Ram & Hari Gopal, 1981; Campbell, 1985; Nelson, 1994; Widmer, 1998). The outstanding example of periodicity is the seven documented mass-flowering events since 813 AD of a Japanese bamboo which are at intervals or multiples of 59–63 years (Kawamura, 1927). A fixed periodicity to bamboo flowering has striking parallels in the shrub genus *Strobilanthes* Blume (Janzen, 1976) and periodical cicadas (Williams & Simon, 1995). Kawamura (1911-12, cited in Kawamura, 1927) proposed that periodicity in bamboos must be the product of an endogenous mechanism relatively immune to environmental influences. This hypothesis is supported by observations of synchronous flowering by parental stock and transplanted seedlings and vegetative off-shoots (Troup, 1921; Kawamura, 1927; Seifriz, 1950; Watanabe *et al.*, 1982; Tanimoto & Kobayashi, 1998) even when the transplantation is across major climatic zones and the age of the parent and offshoot varied markedly (Janzen, 1976). Suggestions that environmental phenomena such as sun-spot activity and drought cycles may initiate flowering (Wong, 1981; Campbell & Qin Zisheng, 1983; Campbell, 1985) lack convincing generality (Brandis, 1899; Troup, 1921; Seifriz, 1950; Gadgil & Prasad, 1984). Kawamura (1927) noted that co-existing species each had a unique flowering schedule, which is also problematic for explanations invoking environmental cues. The endogenous mechanism hypothesis, hereafter referred to as a biological clock, has been accepted by many (Troup, 1921; Janzen, 1976; Simmonds, 1980; Keeley & Bond, 1999) but not all (Campbell, 1985). Simmonds (1980) noted that the evidence is "anecdotal and scrappy" but nevertheless persuasive. The case has recently been strengthened by Tanimoto & Kobayashi (1998), who documented that flowering transplants of a Japanese bamboo did so at the same time as their parent population, but that non-flowering transplants were from a parent population that did not flower.

Although the nature of the bamboo clock remains unknown, recent evidence has elucidated the genetics and function of biological clocks in shorter-lived plants. Biological clocks are mechanisms that control functions external to themselves (Rensing *et al.*, 2001), for example by initiating the production of hormones when a threshold value of some phenomenon is reached. Most attention has been focussed on cyclic mechanisms such as the circadian clock (see Samach & Coupland, 2000; McClung, 2001 and McWatters *et al.*, 2001 for recent reviews), but linear or "hourglass" biological clocks interact with physiological responses to growth and the environment to determine the onset of phases of development in many organisms (Lawson & Poethig, 1995; Pourquie, 1998; Rensing *et al.*, 2001). A developmental stage may be triggered when a clock reaches a threshold chemical or biological state, and the rate of progression towards that threshold may be dependant on external factors such as temperature as well as internal metabolic or chemical activity (Rensing *et al.*, 2001). A genetic basis for linear clocks has been demonstrated in annual plants (Telfer & Poethig, 1998; Schomburg *et al.*, 2001; Rouse *et al.*, 2002; Zhang & van Nocker, 2002). In a range of environmental and evolutionary contexts, selection can be expected to favour varying interactions between exogenous cues to, endogenous cues to, and genetic predetermination of development times. The Birch *Betula verrucosa* Ehrh. seedlings of Longman & Wareing (1959) may represent an extreme in which physical state determines the onset of flowering. Bamboos appear to represent an alternate extreme, in which genetic predetermination in the form of a linear biological clock that is relatively immune to external influence is dominant. In a variety of plants, vegetative maturity and the onset of reproduction can become uncoupled (Lawson & Poethig, 1995), as they are in semelparous bamboos.

Janzen (1976) proposed that the flowering distribution is the product of stabilizing selection acting on genetic variants of the clock, in which intense predation of seeds during non-gregarious flowering, and predator satiation with gregarious flowering, strongly favours synchrony. In mast-fruiting, iteroparous plants and especially those that are wind-pollinated as most bamboo appear to be (e.g. Nadgauda *et al.*, 1993; John *et al.*, 1995), synchrony may also be advantageous in improving outcross pollination rates (Kelly *et al.*, 2001; Koenig & Ashley, 2003). Keeley & Bond (1999) suggested that synchronous death of the parent generation may promote extensive wildfires that create canopy gaps for seedlings, whilst Pearson *et al.* (1994) suggested that it provides release from shoot parasites. Satiation of seedling browsers (Prasad, 1985) could also drive stabilizing selection.

However, the biological clock hypothesis alone does not explain the diversity of flowering patterns in semelparous bamboos. Neither adaptive value nor mechanisms have been demonstrated or even clearly hypothesized for the flowering wave or other more diffuse patterns of synchronised flowering. Janzen (1976) suggested that flowering waves are derived from synchronous populations when humans introduce species to environments lacking the selection pressure (seed predators) for synchrony, though it is unclear how such relaxed selection could produce the spatial patterning of a flowering wave. In contrast, Gadgil & Prasad (1984) argued that asynchrony is the normal state in semelparous bamboos with synchrony a state achieved only under special circumstances, and that human disturbance was not implicated in spatially-structured flowering waves in

India. The discovery of a flowering wave in a remote section of Amazonia (Nelson, 1984) appears to rule out a major role for human disturbance, particularly in the form of horticultural selection and transplantation. Banik (1998) and Stern *et al.* (1999) suggested that bamboo flowering waves are spatially-directed, but Gadgil & Prasad (1984) demonstrated using historic data that this is not always so. Nelson (1994) and Jaksic & Lima (2003) mapped three years of a flowering wave at landscape scales, the former from satellite imagery.

In this study, I provide a multi-scale quantitative description of the spatio-temporal patterns of flowering of *Bambusa arnhemica* F. Muell., a semelparous bamboo from northern Australia, at both landscape- and local-scales, the first such for any bamboo. Landscape surveys were conducted by air, boat and ground surveys throughout the range of the species. Using the insights gained, I then offer hypotheses about the interaction of endogenous and exogenous cues to flowering that may lead to the development of flowering waves and other flowering patterns in bamboos.

Study area and species

Bambusa arnhemica is endemic to the north-west of the Northern Territory, Australia, between latitudes 11° and 14° South and longitudes 130° and 133° East, where it is the sole bamboo species (Liddle *et al.*, 1994; Franklin 2003). Approximately 15% of the range of *B. arnhemica* including almost the entire catchment of the South Alligator River is contained within the World Heritage Kakadu National Park (Fig. 1). The climate is monsoonal tropical, with high temperatures throughout the year. Mean annual rainfall ranges from 1200 mm in the south-east to 1800 mm in the north-west, with *c.* 90% falling in the five months from November to March and virtually nil from mid-May to mid-September. The region's vegetation is predominantly a wooded eucalypt savanna in which linear riparian forests, and occasionally other vegetation types, are embedded (Fox *et al.*, 2001). Soils are mostly infertile and often lateritic and/or skeletal except in areas of fluvial deposit. The region has a long history of geological stability, but during Quaternary glaciations has been subject to major fluctuations to climate and sea levels (Williams, 1991). Human occupation of the area has been continuous since Aboriginal people entered the area *c.* 50,000 years ago, with European settlement commencing in the 1840s. However, the human population remains sparse, and the natural landscape is essentially intact but for small pockets of agricultural development and the urban area of Darwin (population 90,000).

Bambusa arnhemica is a 10-20 m tall, clumping bamboo (Franklin, 2003). It occurs mostly on six major and several minor river systems, along which it is patchily distributed but often abundant to the point of forming mono-dominant bands within riparian forests extending for many kilometres (Franklin & Bowman, in prep.). Much less frequently, it also occurs as isolated small stands on coastal headlands, rocky hillsides and in other non-riparian situations (Franklin & Bowman 2003, in prep.). Flowering mostly commences in June or July and continues until the onset of wet-season rains in about November (DCF, unpubl. data). The indigenous Aboriginal population made use of the species for fishing spears and other implements, and traded bamboo extensively (Berndt & Berndt, 1988; Bindon, 1991; Marrfurra *et al.*, 1995; Raymond *et al.*, 1999), but there is no indication that *B. arnhemica* stands have ever been manipulated or dispersed by humans.

Definitions

In this paper, the term "synchronous flowering" is used to describe observations of flowering in the same year by the majority of culms, adjacent clumps (genets) or stands at any spatial scale. Critically, it does not imply synchronicity across an entire species. The term "mass-flowering" is interchangeable but is usually applied at larger spatial scales such as when the majority of clumps over areas of hectares or greater, or adjacent stands of clumps, flowered in the same year. A spatially-coherent group of clumps or stands of clumps that flower synchronously is termed a "(flowering) patch". The term "scattered flowering" is applied to single clumps or sometimes two or three adjacent clumps that flower in a different year to their neighbours, or more generally to a number of clumps flowering simultaneously which are dispersed through a stand of clumps, the majority of which are not flowering. The terms "gregarious" and "sporadic", common in the bamboo literature, are reserved for discussion of reproductive strategies.

Methods

Landscape-scale surveys

All major primary, and numerous smaller watercourses within the range of *Bambusa arnhemica*, along with 27 non-riparian stands, were surveyed for the occurrence of mass flowering and die-off by air, boat or land. Most areas were surveyed in 2000–01. Areas in which mass-flowering was not detected in the initial survey were re-surveyed in 2001–02 and iteratively if required in 2002–03, along with a few additional areas. All air and boat surveys, and most land surveys, were conducted during the wet season during or soon after the flowering season (see *Results*) when all live clumps that were not flowering were in full leaf, and flowering or recently-flowered clumps appeared yellow, contrasting sharply with the green landscape.

Accessible areas were surveyed quantitatively from land or by boat. Quantitative assessments (n = 807) were of the status (leafy, flowering, dead, or combinations of these) of the first ten mature clumps encountered beyond a pre-specified point, using 10 x 42 mm binoculars when required. The remains of dead clumps remain standing for several and often up to five years after flowering. During linear surveys along watercourses, assessments were mostly conducted at one kilometre intervals. The location of assessments was recorded using a Global Positioning System (GPS).

Much of the range of *B. arnhemica* is not readily accessible by road or boat, especially so during the wet season. Inaccessible areas were surveyed from a single-engine, fixed-wing-above aircraft flying at 150 kmh^{-1} and 150 m above the ground, a height at which the status of bamboo clumps was readily apparent. Flights generally tracked riparian systems. A GPS operator recorded a waypoint every 30 seconds (n = 1749 with bamboo present excluding repeat surveys, n = 2302 in total), corresponding to a 1.3 km segment of riparian vegetation, and conveyed the waypoint number to an observer (always the author). For each segment, the observer made a qualitative assessment of the relative abundance of leafy, flowering and dead bamboo in whole numbers summing to ten, and a qualitative assessment of the abundance of bamboo on a scale of 0–10 in which a score of 3 corresponded to the presence of at least 10 clumps in the segment.

At two riparian patch boundaries, Bridge Creek (13°25'S, 131°19'E) and Adelaide River (12°55'S, 131°15'E), quantitative assessments (as above) were made at 100 m intervals (as determined by GPS) over a three kilometre section of watercourse. At Bamboo Creek (12°55'S, 131°10'E), the position of a series of small non-riparian bamboo stands were plotted in August 2001 by following stand boundaries whilst taking a GPS reading every 10–20 m. Discrete flowering patches were readily identified and ascribed to a year of mass flowering based on the status of > 95% of the clumps at the time and during prior observations at the site.

Mapping landscape-scale patterns

Ground surveys along the Adelaide River produced qualitatively identical but quantitatively different results to an air survey (Table 1). Lower mean scores for the air survey are as anticipated because even one non-flowering clump in a 1.3 km segment reduces the score to nine. There were significant qualitative as well and quantitative differences for the Daly River survey, where unusually (see *Results*) only 56% of clumps flowered in the year of survey.

Quantitative and qualitative assessments were converted to principal states (dead, flowering or leafy), combined, and mapped in ArcView GIS 3.2a (ESRI, 1992-2000) using only assessments with at least 10 clumps. Stands that were predominantly dead in 2000–01 were attributed to mass flowerings in the period 1996–99 based on historic records which were actively sought from Herbarium specimen labels and observers. A small number of predominantly dead stands that were first encountered after 2000–01 were excluded from the analysis unless they could be confidently attributed to a year of mass flowering.

Table 1: Comparison of quantitative (ground or boat) and qualitative (air) surveys of flowering in *Bambusa arnhemica* F. Muell.

"%disc." is the percentage of assessments discarded from *n* from prior to analysis because fewer than 10 clumps were recorded.

"%flow." is the percentage of assessments (after discarding small samples) in which flowering was the predominant state.

The Fisher's Exact Test is two-tailed and compares the proportion of assessments in which flowering was the predominant state. The *t*-test compares mean flowering scores from the two methods.

Location	Year	Technique	n	%disc.	%flow.	Fisher's Exact Test	flowering score (mean ± s.e., x/10)	*t*-test (2-tailed)
Daly River	2000	boat	97	2.1	64.9		5.58 ± 0.189	$t = 3.94$
		air	61	16.4	82.4	$P = 0.035$	6.88 ± 0.281	$P = 0.0001$
Adelaide River	2001	ground	17	0	100		9.38 ± 0.225	$t = 3.12$
		air	17	0	100	*not testable*	8.35 ± 0.242	$P = 0.004$

Temporal patterns within a flowering patch

Temporal (between-year) patterns are described for an 18-kilometre linear stand of riparian bamboo on the Adelaide River in the vicinity of Tortilla Flats (13°06'S, 131°14'E) that mass-flowered in late 2001. Six transects, each of 100 bamboo clumps, were established at intervals of 2 km or more along the Adelaide River by recording starting coordinates with a GPS and proceeding downstream along one bank. Each clump was scored as leafy, flowering and whether this was the first year of flowering, or dead, in each of three consecutive wet seasons commencing with the 2000-01 wet season. In the same area and time period, two sets of 25 clumps were individually tagged and monitored for survival.

Seedling densities

Seedling densities were assessed shortly after germination (*c.* December) under clumps that had recently flowered at Tortilla Flats in the 2000-01 (n = 11 clumps) and 2001-02 (n = 6 clumps) wet seasons, and at Bridge Creek in 2000-01 (n = 4 clumps). At the two sites that had recently mass flowered, the first available clump at 50 m intervals along the river bank was assessed, whereas the site with only scattered flowering clumps, all recently-flowered clumps encountered were assessed. Assessments were at radii of 2, 4, 6 and 8 m from the clump base on each of the four compass points. Seedlings were counted in 30 x 30 cm quadrats, or when at extremely high density, in a 94.5 mm diameter ring placed centrally within the quadrat.

Length of the flowering cycle

Records of previous mass-flowering events were sought from long-term residents and former residents of the area and matched against observations obtained during the current study.

Results

Patterns in the landscape

Mass flowering of *B. arnhemica* stands commenced in 1996 and continued until the end of the study in 2002, during which time *c.* 80% of stands flowered (Fig. 1). Mass flowering occurred in each year of the period with the possible exception of 1997. It commenced in the vicinity of Darwin, and at about the same time in the catchments of the Mary and South Alligator Rivers. The lower, mostly tidal section of the Adelaide River, and stands in the Daly River catchment flowered in 1998, and stands along the Finniss River and further areas of the Adelaide River catchment in 1999. The 2000, 2001 and 2002 flowering events were each mapped in detail (Fig. 1). With very few exceptions, assessments of "no mass-flowering" mean that very little or no flowering was observed.

The assessed states occurred in strongly contagious patches, the largest of which comprised all watercourses in a region of *c.* 3,200 km^2 (in 2000, Fig. 1). In 2001, at least five such patches were identified. The spatial arrangement of flowering patches within the time-sequence was chaotic; there was no single point of origin, nor consistent evidence of radiation or progression across the landscape or up or down catchments. Patch boundaries did not consistently correspond to catchment boundaries or stream junctions, and some boundaries occurred at adjacent points on parallel drainage lines, for example the downstream end of the 2001 patch on tributaries of the Adelaide River system (Fig. 1). The 2000 flowering patch spanned three and possibly four primary catchments. Along watercourses, patch boundaries were variously abrupt or displayed evidence of intergradation and/or outliers at distances of up to one kilometre (Fig. 2). For the most part, stands of *B. arnhemica* on rocky hillsides flowered at the same time as those along nearby watercourses, and no relationship between patch boundaries and soil or parent material types or environmental gradients within river banks was discernible (see also Franklin & Bowman, 2003).

The large scale of Fig. 1 masks some smaller patchiness to as little as 0.2 ha. Small patches were at times embedded within larger patches (see *Patterns within patches*) and exceptionally, a series of small patches formed a flowering sequence in miniature (Fig. 3).

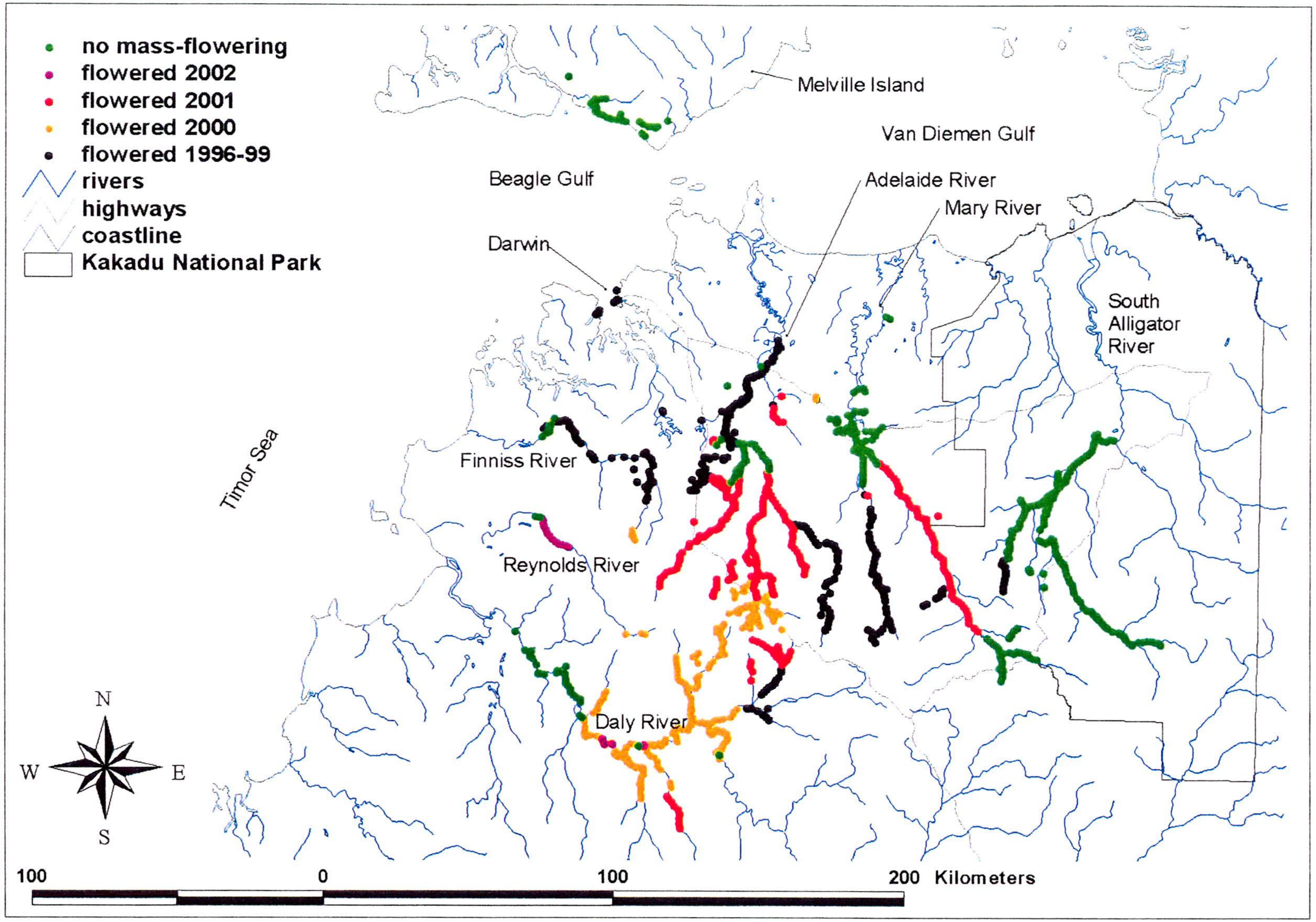


Figure 1: Landscape-scale patterns of mass flowering of *Bambusa arnhemica* F. Muell., 1996 to 2002 based on 2556 assessments.

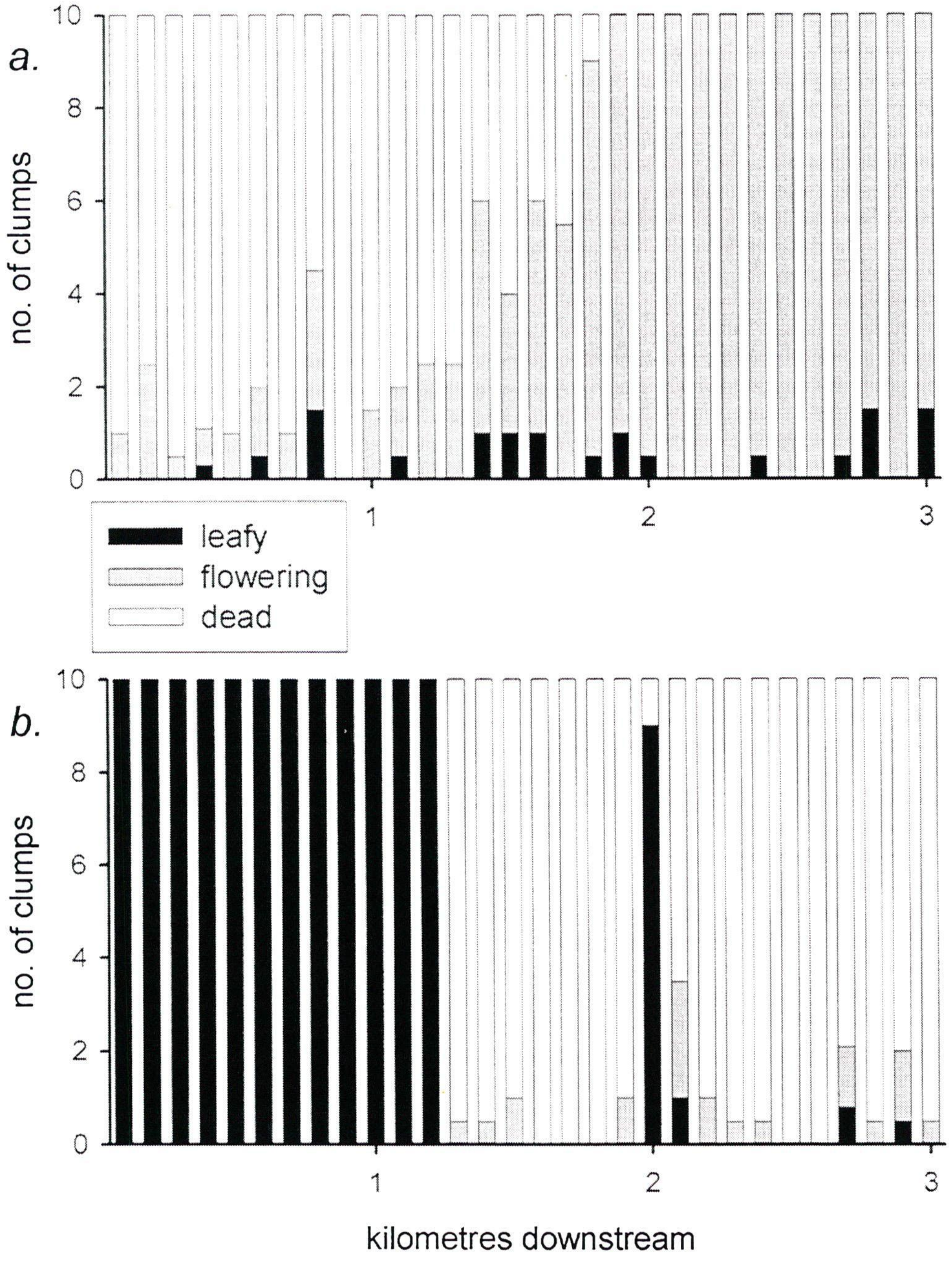


Figure 2: Frequency of leafy, flowering and dead clumps of *Bambusa arnhemica* F. Muell. across patch boundaries, assessed at 100 m intervals in 2001: *a.* Bridge Creek, and *b.* Adelaide River.

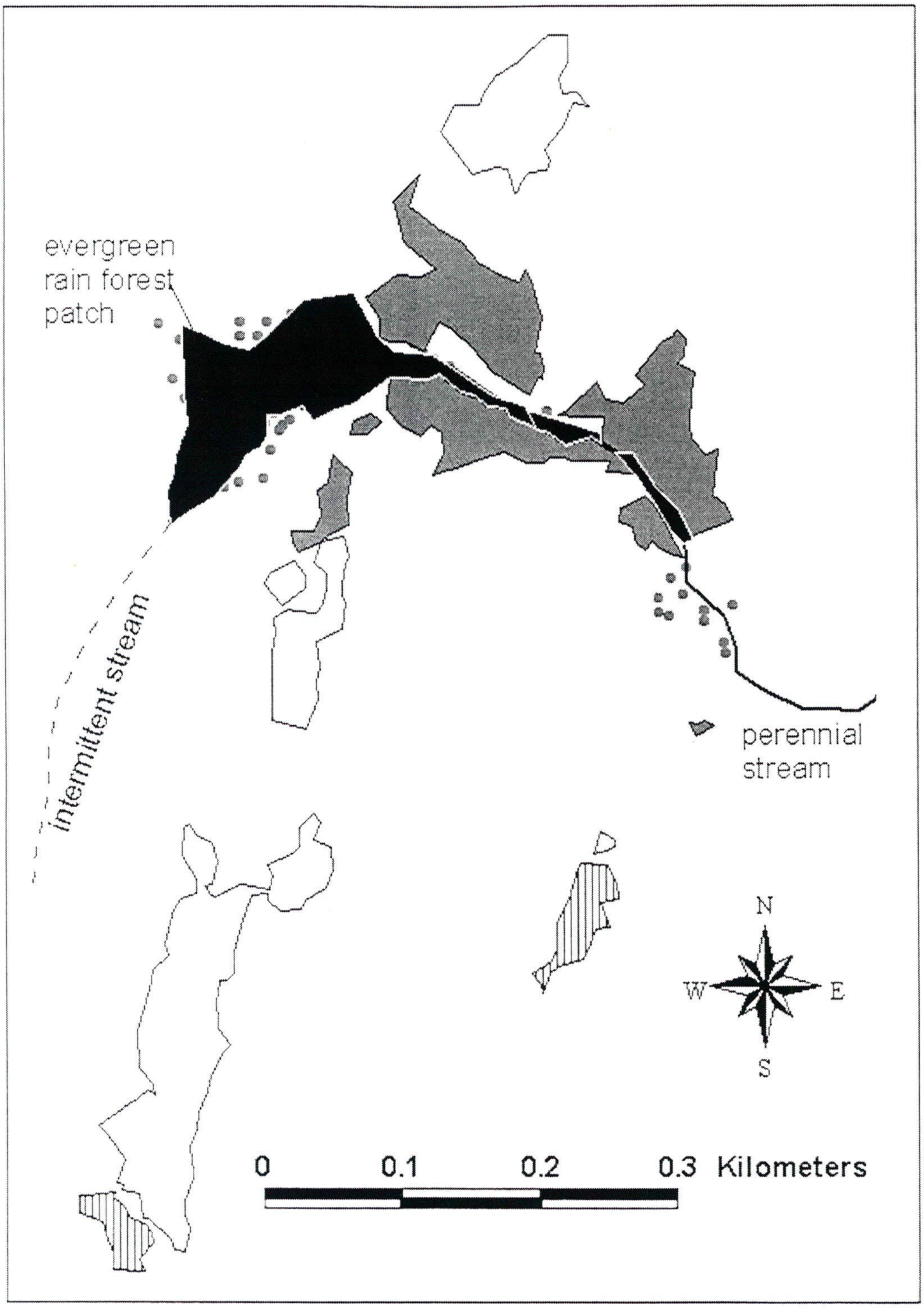


Figure 3: Flowering wave amongst non-riparian patches of *Bambusa arnhemica* F. Muell. at Bamboo Creek.

The grey patches (including scattered dots representing isolated clumps) flowered in 1999, the vertically-hatched patches in 2000 and the outlined white patches in 2001.

Patterns within patches

At Tortilla Flats, 95.7% of clumps initiated flowering in 2001, whilst a few clumps initiating flowering the year before and the year after, a pattern that was remarkably uniform along the sampled 18 km section of the Adelaide River (Fig. 4(a)). More clumps initiated flowering in 2000 than 2002 (1.5% *cf* 0.67%), but the difference was not significant (two-tailed Wilcoxon $T = 3.5$, n = 6, $P = 0.28$). However, more clumps flowered in 2002 than 2000 (Fig. 4(b); two-tailed Wilcoxon $T = 0$, n = 6, $P = 0.03$) because some of the 2001 cohort flowered again in 2002 (see below). A qualitatively similar pattern of marked centrality was evident in most flowering patches (Fig. 5(a,b)).

Thirteen clumps (2.2%) in the Tortilla Flats transects did not flower during the study period (Fig. 4(a)). Of these, twelve were in a single transect and ten of these were adjacent to each other, that transect comprising a non-random arrangement of flowering and leafy clumps (two-tailed runs test, $Z = 3.41$, $P < 0.001$). Thus, the leafy clumps may have constituted an embedded small patch with its own flowering schedule. If this interpretation is accepted for the 10 adjacent clumps and these are excluded from the analysis, then 97.3% of clumps in the main Tortilla Flats patch initiated flowering in 2001.

Along the 96 km section of the Daly River that mass-flowered in 2000 (Fig. 1), 56% of clumps initiated flowering in that year, an estimated 15% in 2001 and 16% in 2002, with 13% remaining leafy throughout the study period (Fig. 4(c)). This more diffuse pattern contrasted strongly with that of tributaries that flowered at the same time, as well as with most other mass-flowering events documented in this study (Figs. 5, 6). Individual quantitative (boat survey) assessment scores along the Daly River in 2000 varied from 1 to 10 (i.e. 10 – 100%) of clumps flowering, with no patterning along the River evident at this scale (two-tailed non-parametric runs test with normal approximation, $Z = 0.36$, $P = 0.72$).

Of 50 tagged clumps, 92% flowered in one season and then died. A few culms on 8% of clumps survived to flower weakly in a second year, after which the clumps died completely; only one of these clumps had carried a non-flowering culm through from the initial year of flowering.

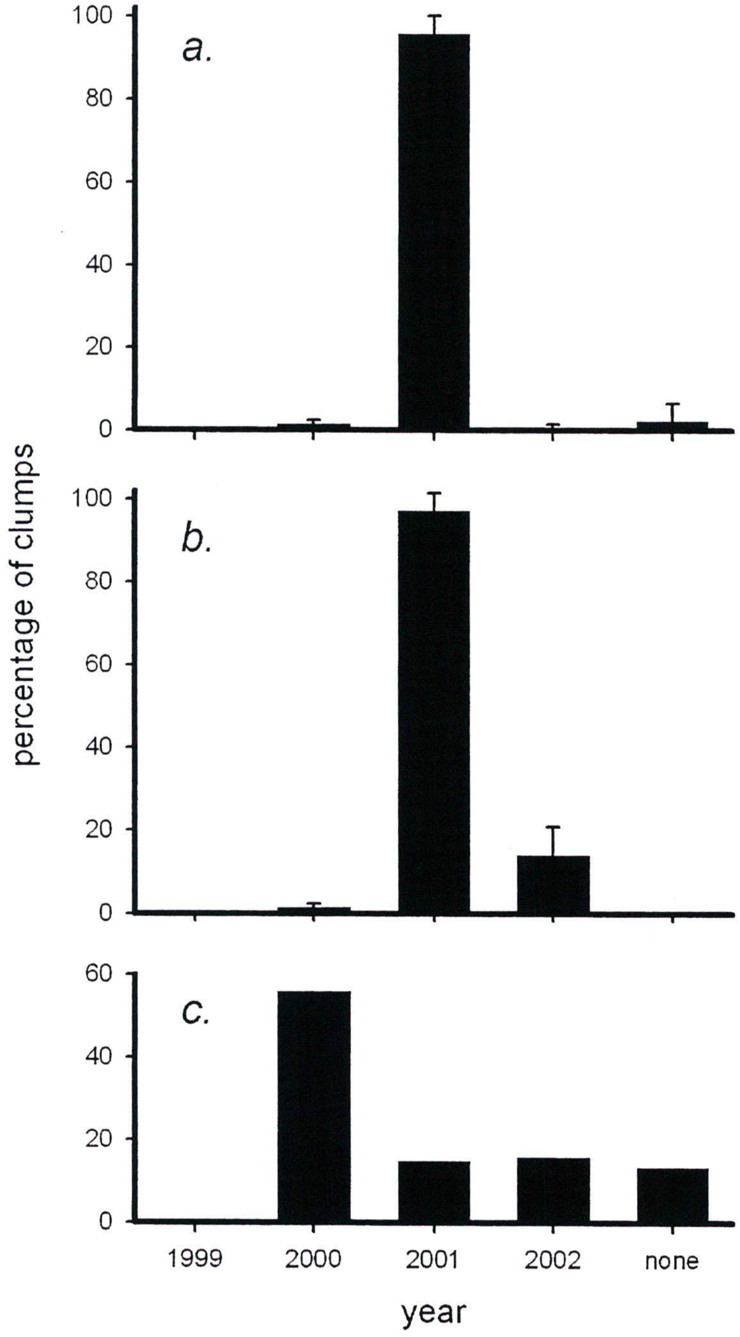


Figure 4: Annual dispersion of flowering by *Bambusa arnhemica* F. Muell. clumps: *a.* that initiated flowering, Tortilla Flats (mean ± s.d.); *b.* that flowered, Tortilla Flats (mean ± s.d.); and *c.* that initiated flowering, Daly River.

The Tortilla Flats estimates are based on repeat assessments of 6 transects each comprising 100 clumps. The Daly River estimate is based on annually-replicated samples of 10 clumps at 1 km intervals, for which there is an unknown error associated with loss of dead clumps between years. "none" indicates no flowering during the study period.

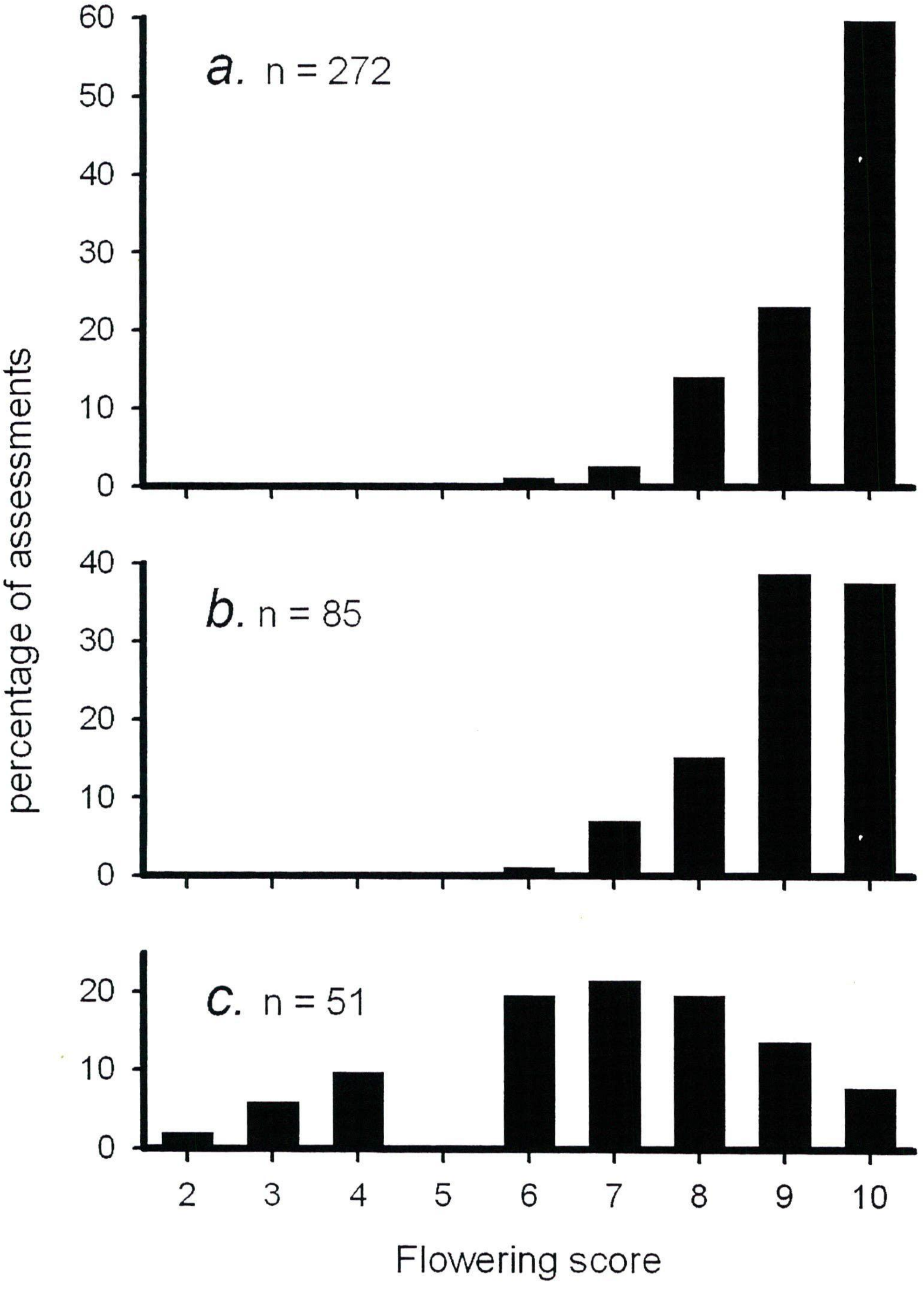


Figure 5: Qualitative (air survey) assessments of flowering (max. score 10 = 100% flowering) within flowering patches of *Bambusa arnhemica* F. Muell.: *a.* all areas except the Daly River catchment during 2000; *b.* tributaries of the Daly River in 2000; *c.* the Daly River in 2000.

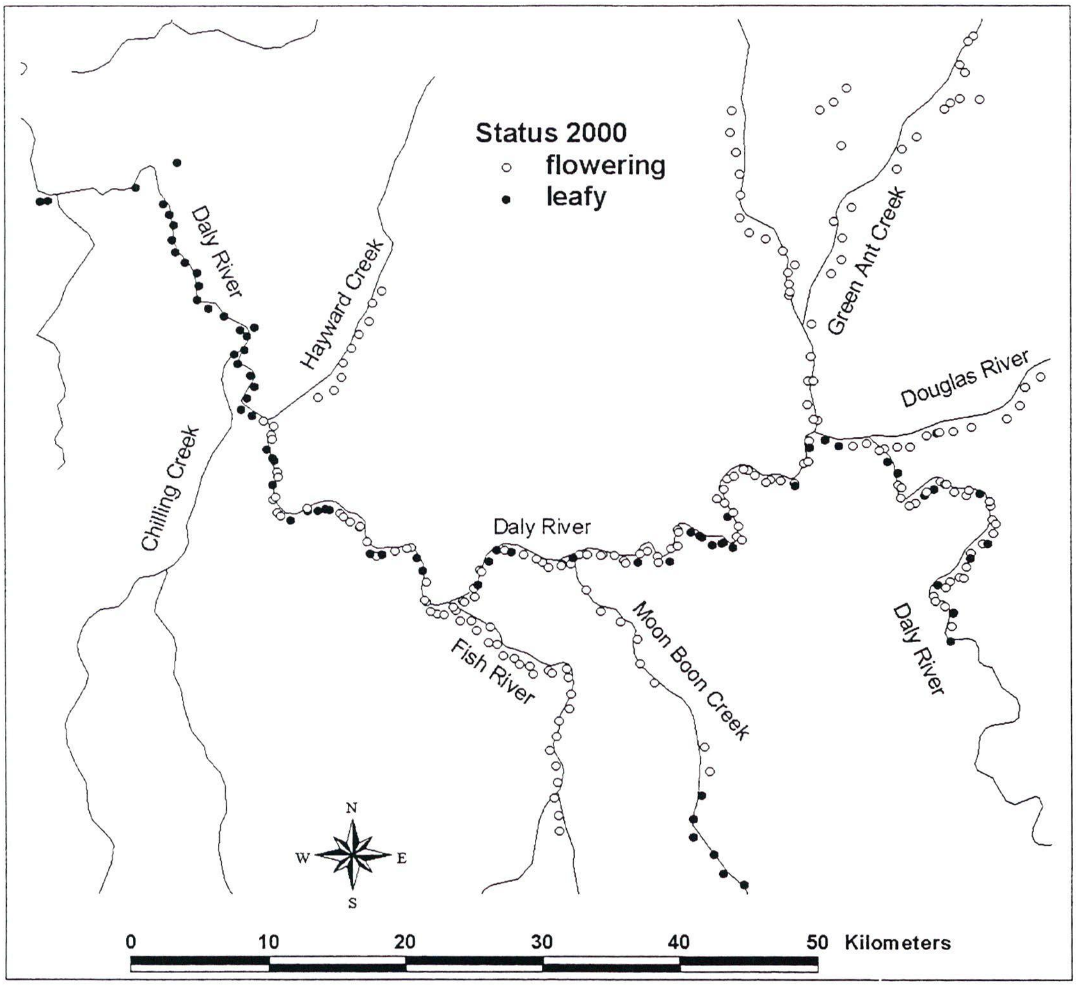


Figure 6: Distribution of flowering and leafy point assessments of *Bambusa arnhemica* F. Muell. along the Daly River and tributaries in 2000.

Assessments are of majority status and do not necessarily imply that all or even nearly all clumps were in the mapped state. The particularly high density of assessments along the main watercourse is because of the overlap of air and ground surveys (Table 1). Surveys indicate that *B. arnhemica* does not occur along Chilling Creek, nor further upstream along the Daly River.

Seedling densities

Seedlings germinated at three orders of magnitude greater density at mass-flowering sites than they did under scattered flowering clumps (Table 2).

Table 2: Density of germinants under recently-flowered clumps of *Bambusa arnhemica* F. Muell. during and in the year prior to the year of mass flowering.

Location	Year, stand status	Germinant density (mean ± s.d. per m^2)	No. of clumps
Tortilla Flats	2000, year prior to mass flowering	0.89 ± 0.85	11
Bridge Creek	2000, year of mass flowering	1033 ± 514	4
Tortilla Flats	2001, year of mass flowering	2007 ± 627	6

Length of the flowering cycle

I could identify no written records of previous mass-flowering events in *Bambusa arnhemica*, although Bindon (1991 and pers. comm.) reported some flowering in 1986 or 1987 on the lower Mary River, an area that did not mass-flowering during the current study period. Pre-1996 herbarium specimens of *B. arnhemica* flowers were collected from isolated flowering culms or clumps (G. Wightman and M. Parker/Rankin pers. comm.). Oral records indicate that the most recent mass-flowering event prior to 1996 was in 1962 (small seedlings observed in 1963, Table 3) in an area that did not flower during the 1996–2002 study period. Matched historic and recent records suggests that the interval between synchronous flowering, and thus clump longevity, is in the range of 41–51 years (Table 3), the one independently-verified interval being 41 or 42 years.

Table 3: Anecdotal records suggesting the length of the flowering cycle of *Bambusa arnhemica* F. Muell.

All historic records are based on personal communications between the observer and the author. All recent observations are the author's.

Location	Historic record	Recent observations	Flowering cycle (yrs)
Adelaide River at Acacia Gap	R. Petherick: mass-flowering and die-off in 1948	mass-flowered 1998 or 1999	50 or 51
Reynolds River at Welltree Station	R. Petherick: mass-flowering and die-off in the period 1953 – 1955	mass-flowered 2002	48 ±1
Adelaide R. at town	J. Haggard: mass-flowering in period 1955 – 1959	mass-flowered 2001	44 ± 2
Coomalie Creek	L. Ah Toy: mass-flowering during childhood, est. 1949 – 1959	mass-flowered 1998	44 ± 5
headwaters Adelaide River / Green Ant Ck.	F. Woerle: flowering and die-off before 1962, probably 1950s	mass-flowered 2000	44 ± 6
Beatrice Hill & adj. Adelaide River	1. D. Baker: mass-flowering in period 1955 – 1957 2. J. Turnour: mass-flowering in period 1956 – 1959	mass-flowered 1998	41 or 42
lower Mary River	T. Baldwin: no mass-flowering or die-off in 41 years	no recent mass-flowering	> 41
Talc Head	1. C. Fitzgerald: mature clumps present 1956; no flowering til recent 2. R. Maxwell: mature clumps present *c.* 1972; no flowering til recent	mass-flowered *c.* 1996	> 40
Mary River at old ford	A. Wilson: clumps all dead, seedlings 20–25 cm tall, 24/8/1963	no recent mass-flowering	> 40
Adelaide River at Tortilla Flats	1. G. Melville: no mass flowering or die-off 1962 – 1991 2. J. Sullivan: no mass flowering or die-off 1964 – 1980	mass-flowered 2001	> 39

Discussion

Patterns of flowering in B. arnhemica

Bambusa arnhemica is strictly semelparous, regenerating prolifically from seed (see also Franklin & Bowman, 2003).

Two spatio-temporal patterns of synchrony and asynchrony may be discerned in its flowering. These may be characterised as: *a.* a strongly time-central pattern within flowering patches, corresponding to the peak-and-tails "flowering distribution" described qualitatively by Janzen (1976), and *b.* a succession of flowering patches in consecutive years, the "flowering wave" phenomenon documented in most detail by Gadgil & Prasad (1984).

The flowering distribution within the Tortilla Flats *B. arnhemica* patch was, at a peak of over 95%, markedly more central than the 81.2% peak reported by Filgueiras & Pereira (1988) and the 55.7% and 91.9% of Widmer (1998) for other bamboo species. A strongly central flowering distribution is consistent with the inference from seedling density data that, in *B. arnhemica*, flowering out of synchrony may indeed be seriously disadvantageous (Janzen, 1976). Though there is a considerable body of anecdotal evidence to this effect (reviewed in detail by Janzen, 1976), there is little quantitative evidence. Taylor & Qin Zisheng (1988) reported that 34% of florets in a mass-flowering year produced seed, whilst only 0.6% did the year after. Gonzalez & Donoso (1999) reported 5% seed viability from bamboo clumps in the flowering tails but 60–90% viability from those that flowered synchronously. In no case is it clear whether the difference is attributable to seed predation, pollination failure or other causes. Nor is it clear that reduced seed or seedling production necessarily leads to reduced recruitment of reproductive adults, as reported rates of potential recruitment under asynchrony may still exceed the replacement rate. As predicted by Janzen (1976) on the basis of hypothesized selective pressure by seed predators whose populations may expand during the course of a flowering event, the leading tail was larger than the following tail, though not significantly so. Curran & Webb (2000) reported that seed predators destroyed all seed that remained after a dipterocarp mast-fruiting and germination event.

The uncharacteristic flowering distribution along the Daly River, along with confinement of the unusual pattern to the main watercourse and the lack of strong differentiation of this diversity into smaller patches, suggests that exceptionally severe flooding 30 months prior to the onset of mass flowering may have disrupted the event. The Daly River is the largest watercourse in the study area by almost an order of magnitude, with a 52,600 km^2 catchment (Jolly, 2001) that extends well beyond the mapped area, there being no known stands of *B. arnhemica* in the middle and upper catchment (Liddle *et al.*, 1994). Cyclonic rains in the upper catchment in January 1998 produced exceptional flooding even by the flood-prone standards of a monsoonal system. The town of Katherine in the mid-catchment was devastated by a flood peak of 20.4 m (KRW, 1999), substantially in excess of the 19.10 and 19.27 m that correspond to the predicted 1:50 and 1:100 year exceedence probabilities (NTES, 1990). Further downstream within the range of *B. arnhemica*, the peak flow was 20% greater than at Katherine (Jolly, 2001), massive river-bank erosion ensued, and at least some *B. arnhemica* clumps appeared to have been torn off at ground level (pers. obs.). Downstream tributaries occupied by *B. arnhemica* were exempt from the extremes of the flood because the heaviest rainfall did not occur within their catchments.

The flowering wave in *B. arnhemica* was markedly non-random in that, after more than three decades of near-total inactivity, mass-flowering occurred in most or all years from 1996 to at least 2002, with one or more patches flowering in each year. Gadgil & Prasad (1984) reported that a bamboo flowering wave extended over 5–6 years. As in that study, the flowering wave in *B. arnhemica* did not coincide with drought, the period being one of mostly average to very-much-above average wet seasons throughout the study area (CBOM, 2003). The spatially-chaotic nature of this flowering wave contrasts with the spatially-directed flowering waves reported by Ne Win (1951), Soderstrom & Calderon (1976), Banik (1998) and Stern *et al.* (1999). Gadgil & Prasad (1984) tested an earlier claim of spatial direction in the flowering of an Indian bamboo and found a lack of spatial direction similar to that reported here.

In contrast to the five-fold variation in the size of patches reported by Gadgil & Prasad (1984), in this study patch size varied by more than four orders of magnitude, a result which could be a simple product of greater available resolution. Some smaller *B. arnhemica* patches were of similar size to the 1–100 ha patches reported for a "sporadic-flowering" bamboo (Campbell, 1985), and at least some accounts of "sporadic" flowering are of small patches rather than isolated culms or genets (Gadgil

& Prasad, 1984; Pearson *et al.*, 1994). The ecological distinction between large- and small-scale synchrony drawn by Gadgil & Prasad (1984) may therefore be quite arbitrary, and its ecological relevance remains to be established. Seed predators need only be satiated at a scale larger than that at which they operate (Lalonde & Roitberg, 1992) and pollination efficiency is likely to be improved at quite local scales in wind-pollinated species (Knapp *et al.*, 2001; Sork *et al.*, 2002). However, Curran & Leighton (2000) and Curran & Webb (2000) found that predator satiation in a dipterocarp mast-fruiting event occurred at larger, landscape scales.

There is no evidence of, nor reason to suspect a human role in the creation or structure of the *B. arnhemica* flowering wave. It is also difficult to imagine how the flowering wave could have arisen in direct response to edaphic patterns or climatic cues. Analyses in search of climatic or other one-off environmental cues appear pointless because they demand an unlikely assumption – that the observed sequence is primarily the product of events associated with the previous generation of bamboo. Flowering waves are widely reported amongst bamboos (Gadgil & Prasad, 1984), and are repeated in successive generations (Banik, 1998). A reasonable starting point for their interpretation is that they developed in each species either over a number of generations or during a single historic event.

Development of a flowering wave

I propose that bamboo flowering waves are the product of environmentally-induced increments to flowering schedules in which the underlying periodicity, reset at germination by an endogenous biological clock, is maintained. When part of a population is subject to such an increment, and that part is sufficiently aggregated in time and space to maintain the viability derived from synchronicity, an off-set (patch) is established that will be maintained across generations. An accumulation of increments produces a flowering wave.

What processes could cause increments to bamboo flowering schedules without altering their fundamental periodicity? At least two possibilities are worth considering as hypotheses for future research.

Stressors on the plant that override or force the clock, for example by triggering hormone production independently of the clock, might initiate flowering. Conceivably stressors could also suppress flowering by suppressing hormone production that the clock has initiated. In many bamboos, selection appears to have favoured dominance by the clock over physiological circumstances or stress, but such dominance need not be absolute (Lawson & Poethig, 1995). Bamboo clumps severely damaged by roadworks may flower out of synch with their undisturbed neighbours (Brandis, 1899; Mohan Ram & Hari Gopal, 1981; DCF, pers. obs.). In periodical cicadas, stress due to crowding has been hypothesized to cause a one-year delay in emergence (White & Lloyd, 1979). It is possible that the threshold of physiological stress required to induce flowering decreases as the scheduled time of flowering approaches.

The events described on the Daly River suggest that environmental perturbations in the period shortly prior to a scheduled flowering may influence flowering time. In the context of *B. arnhemica*, severe flooding, fire or cyclone damage appear likely candidates. However, the Daly River event failed to produce temporally coherent off-sets at even quite small spatial scales. Sorting based on selection for localised synchronicities might, over a number of generations, lead to more evident spatial coherence and even in the long-term to the re-emergence of one or several large patches.

However, a mechanism that is able to uniformly alter flowering schedules over large areas may provide a more general explanation for bamboo flowering waves. The bamboo clock may be "counting" environmental periodicities such as seasonal variation in temperature or moisture, and thus be prone to "mis-counting" in the event of environmental irregularities or perturbations. Mass-flowering of a montane Chinese bamboo in the early 1980s was confined to stands below 3,200 m (Taylor *et al.*, 1991), suggesting a possible effect of temperature (see also Widmer, 1994). Late frosts have been postulated to cause periodical cicadas to "count" two winters instead of one and emerge a year early (Alexander & Moore, 1962; Martin & Simon, 1990). Such irregularities are likely to occur at a range of spatial scales and often over large areas, more or less uniformly affecting adjacent bamboo genets and stands. Conceivably, the spatial scale could even include the entire population, producing the constrained variation in observed periodicities that has been reported.

In this hypothesis for the development of a flowering wave, the pre-eminent role of stabilizing selection for synchrony which Janzen (1976) postulated as driving both the flowering distribution and the evolution of semelparity in bamboos is retained, but the spatial scale of synchrony is progressively reduced over generations by stochastic events. This contrasts with Janzen's (1976) hypothesis that relaxation of selection for synchrony is necessary for a flowering wave to develop. If off-sets were the result of change to or variation in the underlying periodicity, temporal chaos rather than an ordered flowering wave would result within a few generations, as demonstrated in a modelling study for periodical cicadas (Lloyd & Dybas, 1966, Fig. 2). This hypothesis also contrasts with Gadgil & Prasad's (1984) suggestion that large-scale synchrony is an infrequent, secondary state in bamboos that arises only within continuous distributions in reliable climates. Simmonds (1980) argued that secondary development of synchrony by incremental natural selection would be difficult in a long-lived organism because populations would have to pass through a maladaptive phase of semi-synchrony. Semelparity may itself promote synchrony (Young & Augspurger, 1991).

A general and dynamic hypothesis for the huge range of flowering patterns in semelparous bamboos is suggested, in which synchrony is the primary state. Synchrony is maintained by stabilising selection (Janzen, 1976) and the lattice pollination effect (Satake & Iwasa, 2002), and spread by dispersal (Troup, 1921). However, it is fragmented by off-sets and disrupted by processes as yet unknown which alter the genetic integrity of the biological clock. The flowering patches thus created are incipient, allochronic species, a suggestion with strong parallels to a postulated speciation process in periodical cicadas (Martin & Simon, 1990; Simon *et al.*, 2000; Cooley *et al.*, 2001). With speciation and dispersal, synchrony is renewed.

Suggestions for further research

Our understanding of bamboo life histories is founded largely on anecdote, study being hindered by the infrequency and general unpredictability of the phenomenon, long generation times, and also the oft remoteness of the events from centres involved in life history research. With the discovery of mass-flowering in relatively undisturbed areas such as the Brazilian Amazon (Nelson, 1994) and northern Australia (this study), Janzen's (1976) pessimism that human disruption was destroying the opportunity to study the phenomenon appears unwarranted. If we are to make further progress, focussed quantitative studies are required, as previously suggested by Simmonds (1980), Young & Augspurger (1991) and Kelly (1994) but rarely undertaken. This study suggests a number of tractable options.

The adaptive value of synchronicity and the processes driving it in bamboos remains to be quantitatively identified. There is ample precedence for such studies in mast-fruiting plants (Silvertown, 1980; Augspurger, 1981; Nilsson & Wastljung, 1987; Koenig *et al.*, 1994; Curran & Leighton, 2000; Kelly *et al.*, 2001; Shibata *et al.*, 2002) and periodical cicadas (Karban, 1982; Williams *et al.*, 1993). Disentangling the roles of predator satiation, increased pollination efficiency and other possible effects may be best undertaken within massive flowering events, but a key issue in bamboo biology would appear to be whether these effects continue to operate when synchrony occurs at smaller spatial scales. The greater frequency of the latter should facilitate such a study. The hypotheses here generated suggest that synchrony will remain adaptive regardless of its scale.

This hypothesis for the development of flowering waves also suggests that the spatio-temporal patterns of flowering within a wave should be repeated in successive generations with only incremental variation. With two generations of data, the cause of any increments may then be discernible. *Bambusa arnhemica* stands that flowered in this wave are unlikely to flower again before 2036, but some other species may become available sooner. The detectability of large-scale die-off from satellite imagery suggests that the pattern described by Nelson (1994) for bamboo in the Brazilian Amazon in the late 1980s could be expanded retrospectively in both time, spatial scope and resolution. As the species involved, *Guadua weberbaueri* and *G. sarcocarpa*, appear to have flowering cycles of 26 – 29 years (Nelson, 1994), a repeat may be anticipated to commence in about 2015.

Postscript

At the time of writing (late 2003), mass-flowering of *B. arnhemica* is reported to be occurring in a small area of Kakadu National Park, with widespread, scattered flowering along the downstream, non-tidal section of the South Alligator River hinting of a possible mass-flowering in 2004. This extends the flowering wave to eight, and potentially nine years.

Acknowledgements

David Lawson realised the value of the opportunity presented by mass-flowering in *Bambusa arnhemica*, and arranged generous funding for surveys through the Parks & Wildlife Service (Northern Territory). Supplementary funding was provided by the Key Centre for Tropical Wildlife Management. Julian Gorman, Philip McMahon, James Smith, Simon Stirrat, Richard Luxton, Jenny Koenig, Renee Bartolo, Dan McIntyre, Aaron Petty and Robert Taylor assisted with air and boat surveys. The low-level flying skills of Dale Franke, Matthew Johnson and Phil Rofe were much appreciated. Siripong Gumthira and Carmen Verhagen assisted with the assessment of seedling densities. David Bowman provided an invaluable sounding-board for and source of ideas about the presentation of this manuscript. Peter Whitehead, Mark Gardener, Caroline Lehmann and Guy Pardon commented helpfully on a draft.

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Chapter 6:

Canopy and culm shoot phenology

This chapter has been submitted as:

Franklin, DC. Canopy and culm shoot phenology of a facultatively-deciduous bamboo in an intensely monsoonal climate.

Abstract

Canopy fullness, leaf flush and the process of culm recruitment were documented for the vegetatively-mature life phase of a semelparous, clumping bamboo. Three sites along an edaphic gradient in the Australian monsoonal tropics were monitored monthly for 2.5 years. *Bambusa arnhemica* was facultatively deciduous, remaining evergreen in moist situations close to permanent water, but suffering total loss of canopy for up to four months during each dry season on a hillside. Leaf flush occurred promptly and rather briefly after the first showers of the wet season at two riparian sites, earlier following a dry-season fire, and later at the hill site. Culm shoots emerged soon afterwards, but the major phase of culm elongation took place during the middle and late wet season. Culm elongation rates peaked at 20–30 cm/day. Culm recruits commenced branching and foliation shortly before or after the completion of elongation, but this activity was deferred until the following wet season on most clumps at the drier site. Not all culms completed elongation before the onset of the dry season, and those that didn't remained permanently stunted. The bamboo growth form differs fundamentally from that of dicotyledonous trees, providing considerable flexibility in responding to unpredictable pre- and post-monsoonal rains. However, culm elongation must be completed in a single wet season, a commitment made possible by the predictably heavy monsoonal rains but constrained by the length of the dry season.

Introduction

Monsoonal (wet-dry) tropical climates pose particular challenges for long-lived plants, but also provide particular opportunities. The annual alternation between extremes of wetness and dryness may demand physiological compromises and limit phenological options. Rainfall during the early and late stages of the wet season is notably unreliable (Cook & Heerdegen 2001). However, temperature rarely limits growth, and monsoonal rainfall during the middle of the wet season is exceptionally predictable and heavy (McDonald & McAlpine 1991), ensuring annual saturation of the soil and renewal of subsoil moisture reserves.

A surprisingly wide range of phenological patterns have been documented amongst trees of monsoonal climates, with major differences between regions (Sarmiento & Monasterio 1983, Eamus & Prior 2001) and, in northern Australia at least, between co-existing species (Williams *et al.* 1997, Bach 2002). Species may be deciduous, semi-deciduous or evergreen, and leaf flush may occur prior to or during the early wet season. However, several generalities seem to hold, including the frequent overlap of phenophases – leaf flush, flowering and fruiting – near the beginning of the wet season (van Schaik *et al.* 1993, Bach 2002), and the cessation of most leaf growth by the middle of the wet season (Eamus 1999), the latter suggesting that resources may be diverted into storage in preparation for the dry season. Another generality appears to be that most deciduous species shed leaves obligately (Eamus & Prior 2001).

In the higher-rainfall regions of monsoonal India, a diverse range of woody bamboos (Poaceae: Bambuseae) are a prominent feature (Troup 1921, Gadgil & Prasad 1984, Tewari 1992). Though often of similar proportions and longevity to dicotyledonous trees and shrubs, bamboos differ in their mode and form of growth and thus, potentially, in their ability to cope with and exploit the monsoonal climate. Bamboos lack the epicormic buds with which most trees renew axis extension after loss of the initial apical meristem due to drought or other stresses (McClure 1966, Sarmiento & Monasterio 1983). Bamboos also lack the deep tap roots characteristic of many savanna trees (Sarmiento & Monasterio 1983). Many bamboos are semelparous, living for many years in a state of vegetative maturity in which growth takes the form of clonal expansion (Janzen 1976, Gadgil & Prasad 1984), increase in ramet size with successive cohorts being confined to the first few years of life (McClure 1966). Bamboo ramets are produced annually and elongate during a single "grand period of growth" (Porterfield 1928) which, in large species, demands growth rates unparalleled amongst vascular plants (Ueda 1960). A feature of this grand period of growth is that culms achieve their mature diameter prior to elongation (Simmonds 1963, McClure 1966). Branching and foliation usually commence only after elongation (Dransfield & Widjaja 1995, Londono 1998), but culm elongation can cause rapid depletion of rhizome carbohydrate reserves (Oshima 1961, Li *et al.* 1998*a*, Zheng BingSong *et al.* 1998), raising questions about their ability to commence the branching process immediately. Mature culms also undertake renewal of foliage (Pearson *et al.* 1994, Li *et al.* 1998*b*), and in some bamboo genera such as *Bambusa*, further development of the branch system (McClure 1966).

The phenological implications of the bamboo growth form for monsoonal climates are little- and incompletely documented. In truly arborescent species, the apparent requirement to complete a massive culm elongation phase within a single period of abundant resources raises questions about the ability of bamboos to fit other phenophases into an annual cycle, and thus their susceptibility to pre- and post-monsoonal climatic variation. In a sub-tropical montane wet-dry climate, culm emergence and elongation coincided with the wet season (Lodhiyal *et al.* 1998), but leaf bud eruption on mature culms occurred prior to the wet season, and leaf expansion slowly and almost throughout the year. In a humid tropical environment with some rain throughout the year, culm emergence occurred before the main wet season, and culm elongation before and during the first part of it, branch development commencing immediately after elongation in some culms but being delayed for a number of months in others (Ramanayake & Yakandawala 1998). In a humid, cool-temperate climate, branch development was delayed until the second growing season (Pearson *et al.* 1994).

In this study, I document phenological patterns in canopy cover, leaf flush and culm recruitment in a 10–20 m-tall clumping bamboo, *Bambusa arnhemica*, from northern Australia, a region with high but acutely seasonal rainfall. Three sites with vegetatively-mature clumps were selected along an edaphic gradient and monitored monthly for 2.5 years. I pose the questions: (1) how do seasonal patterns of canopy retention, leaf flush and culm recruitment in *B. arnhemica* relate to seasonal patterns of rainfall? (2) do leaf flush and culm recruitment phenophases overlap? (3) how rapidly do culms elongate? and (4) does edaphic and between-year climatic variation influence phenological patterns and/or growth outcomes?

Methods

Study area

The study was conducted in the lower Mary River region (12°55'S, 131°39'E) of the north-west of the Northern Territory of Australia, where *B. arnhemica* occurs extensively in riparian vegetation and occasionally on rocky hillsides. The climate is tropical and intensely monsoonal. Daily maximum temperatures exceed 30°C on more than 300 days per year and rarely fall below 25°C. Daily minimum temperatures very rarely fall below 10°C and frosts are unknown. Over 95 percent of the mean annual rainfall of *c.* 1,400 mm falls in the seven month period between October and April, and *c.* 65 percent in the three months January to March, whilst the dry season months of June, July and August each have a median rainfall of zero. More details of the climate are given by McDonald and McAlpine (1991), Williams *et al.* (1997), Cook and Heerdegen (2001) and the Commonwealth Bureau of Meteorology website *www.bom.gov.au.*

Three study sites were selected along an edaphic gradient: (1) on the lower edge of a riparian forest adjacent to a permanent billabong (stranded meander) in the Mary River floodplain; (2) on the upslope margin of the same riparian forest; and (3) on a rocky hillside. These sites are henceforth referred to as *lower riparian*, *upper riparian* and *hill.* Other than persistent water in the billabong, there was no evidence of springs or groundwater at any site that might have been available to bamboo during the dry season. The riparian sites were at Mary River Park, and the hill site was 6.5 km east-north-east on Annaburroo Station.

The Mary River is a perennial river subject to huge seasonal fluctuations in water levels, the catchment area above the study sites being 6,000 km^2. Although 70 km from the sea, the river at Mary River Park is close to sea-level. Soils are deep alluvial clay-loams to cracking black clays. The riparian sites were on a south-facing 5 m bank whose slope varied from 9 – 30°. The vegetation was a riparian mono-dominant bamboo (*B. arnhemica*) forest with scattered riparian trees (*Eucalyptus camaldulensis*, *Corymbia polycarpa* and *Acacia auriculiformis*) and rainforest trees, shrubs and climbers (particularly *Flacourtia territorialis*, *Diospyros calycantha*, *Vitex* sp. and *Ampelocissus acetosa*).

The surrounding country including Annaburroo Station is flat to gently undulating, with a few hills rising to 150 m above sea level. The Annaburroo study site was 35 m above sea level with a south-westerly aspect and slope of 7°, several hundred metres from an ephemeral drainage line and more than 1 km from permanent water. At Annaburroo, *B. arnhemica* was growing on loam with 30 percent surface cover of gravel and small rock (siltstone) of Early Proterozoic origins. The vegetation was a mono-dominant bamboo forest with scattered vine-thicket trees and shrubs, notably *Erythrophleum chlorostachys*, *Helicteres isora*, *Alstonia actinophylla* and *Miliusa traceyi*.

The species

Bambusa arnhemica is a semelparous, pachymorph (clumping) bamboo endemic to the monsoonal north-west of the Northern Territory. It is the sole woody bamboo species in the Northern Territory and one of only three in Australia, bamboo being biogeographically of marginal occurrence on the continent (Franklin 2003*a*). It is primarily a riparian species, but occasionally occurs in vine-thicket formations on hillsides. It is tolerant of inundation by floodwaters for up to a mean of 60 days per wet season (Franklin & Bowman 2003). Clumps are 10–20 m tall and comprise a few to more than 100 culms produced vegetatively during a pre-flowering phase of development that is thought to last more than 40 years. Culms are of highly variable size but typically 4 to 10 cm diameter at 1.4 m, tapering to a fine tip when fully elongated. Branching on the upper culm is of unrestricted monoclade form, so that an indefinite number of branches of variable size may develop from a node, and there are 2–4 (–5) orders of branching. In contrast, the lower branches are usually solitary or trimerous with a dominant central branch, with 2–3 (–5) orders of branching, are often poorly developed and invariably support few leaves. *Bambusa arnhemica* foliage leaves (*cf* the bract-like "culm leaves") are green, 5–20 cm long by 0.8–3.0 cm broad, and grow alternately at nodes of leaf shoots which are mostly less than 40 cm long; leaf shoots are thus terminal branches but of quite different form to larger branches which bear culm rather than foliage leaves. During elongation, leaf shoots are terminated by a needle-like unexpanded leaf *c.* 1 mm in diameter which, at the completion of elongation, expand into a full leaf. For a detailed description and illustration of the species, see Franklin (2003*b*).

As in all bamboos, new ramets arise from buds on older rhizomes that are just below or at the soil surface. When they first appear they are termed culm shoots. Culm shoots are vulnerable to herbivory, and in favourable conditions are "overproduced" such that only a portion of emergent culm shoots develop (Franklin unpubl. data). Successful culm shoots develop a rhizome, root system, culm, branches and foliage. As in all grasses (Atwell *et al.* 1999), culm (and branch) elongation is by intercalary growth, differentiation of the nodes and acquisition of final diameter being completed prior to the major elongation phase (Ueda 1960, McClure 1966). The shoot tip is a robust structure, the emerging shoot in *B. arnhemica* weighing up to 0.5 kg when 30 cm long (Franklin unpubl. data). Bamboo culm shoots, including those of *B. arnhemica*, are prized as a substantial food source for people (*e.g.* Midmore *et al.* 1998, Ito *et al.* 2000, Bhatt *et al.* 2003).

Monthly assessment of leaf and culm shoot state and activity

At each site, ten vegetatively-mature bamboo clumps were selected along a 100 – 200 m long transect. Each clump was assessed in the first week of the month from July 2001 to December 2003, 30 months in total, with the exception of the downslope set in March 2002 and March 2003 when they were inaccessible because of monsoonal floodwaters. Partial interference with the assessment of upper riparian clumps occurred for the same reason in March 2003. Assessments were of canopy fullness (green foliage), leaf shoot activity, number and size class of first-year culms, and distance to surface water. Additionally, development of first year culms was recorded seasonally (see below).

Canopy fullness was assessed in cover classes of: 0 = 0%, 1 = < 2%, 2 = 2–25%, 3 = 26–50%, 4 = 51–75%, and 5 = 76–100%. As a measure of leaf shoot activity, I scanned the canopy of each clump with 10 x 42 binoculars for one minute and estimated the percentage of green leafy shoots that were terminated by an unexpanded leaf, in classes as for canopy fullness above. The number of new culms were scored in size classes of less than 0.4 m (class A), > 0.4 m and < 50 percent of estimated full height (class B), and > 50 percent height (class C). Culm shoots less than 0.4 m are potentially harvestable whereas taller shoots are not, and have not usually commenced their phase of rapid elongation (see *Results*). Class B shoots are in the phase of rapid elongation but are still subject to mortality, whereas class C shoots very rarely suffer mortality during elongation (Franklin unpubl. data). Distance to surface water was recorded in the following classes: not within 5 m, between 0 and 5 m, some but not all culm bases submerged, and all bases submerged. It was not possible to measure the distance to water accurately because the billabong was inhabited by Saltwater Crocodiles *Crocodylus porosus*.

In April 2002 and April 2003, when new culms had completed the elongation phase, one new culm per clump was selected and tagged on the basis that both it and its parent ramet were undamaged, and that the upper culm (foliage and branches) could be viewed. Because of the density of clump canopies, the latter criterion was not met for all clumps, so that 20 culms were tagged in 2002 and 21 in 2003. In each month from then until leaf flush occurred on both the first year and older culms with the onset of the following wet season (November or December), the culm was assessed for elongation, upper and lower branching, and upper branch leaf shoot activity. The elongation categories were: fully elongated or not fully elongated, the latter with an estimate of the percentage elongated relative to nearby culms of similar diameter; culms that were not fully elongated were readily identified because the tip was robust rather than slender. For both lower and upper branches, states were: absent or present; if present, then primary only and < 1 m long, primary only and > 1 m, secondary branching present, or tertiary or greater branching present. Leaf shoot activity was scored as for the entire clump (above).

Measuring culm elongation rates

In the 2001/02 and 2002/03 wet seasons, four and six emerging culm shoots respectively were selected at the riparian sites for measurement of elongation rates. Within seasons, each selected culm was from a different clump, and clumps were distributed evenly between lower and upper riparian areas in the immediate vicinity of, but not necessarily on, the marked clump sets. Only culms from undamaged parent ramets were selected, the resulting culms (measured after elongation) having internode diameters of 6.8 to 9.8 cm at 1.4 m. In 2001/02, culms were selected as they began the phase of active elongation when about 1 m long, and were the first qualifying culm that was accessible for measurement purposes. In 2002/03, I commenced measurements within a week of emergence from the ground. Three culms on each of the six clumps were marked and measured, with subsequent selection of one per clump as it commenced elongation.

There is no satisfactory methodological precedent for the assessment of culm elongation rates in large bamboos. To each culm shoot I fitted a cap consisting of a clear plastic soft-drink bottle with the base cut off. To the cap I attached a measuring tape - in 2001/02 a string with knots at 1 m intervals - in 2002/03 a 30 m free-moving, fibreglass, roll-up tape. In the latter case, the tape-measure casing was attached firmly to a baseplate that was staked into the ground at the base of the culm. Measurements were taken weekly until termination was enforced by either the cap blowing off in a storm, the string or tape breaking or becoming entangled, or floodwaters precluding access to (and destroying) the measuring device. Although there were no quantitative controls, frequent checks during the early stage established the absence of damage to the shoot, and qualitative comparisons with neighbouring shoots over several months suggested no difference in elongation rates.

Analysis

Following Williams et al. (1997), each assessment of the categorical variables canopy fullness and leaf shoot activity were converted to the mid-range of its class prior to analysis. A growth index was then calculated for each clump at each assessment as follows:

$$\text{Growth Index} = \text{canopy fullness} \times \text{leaf shoot activity} \times 100$$

producing an index with a potential range of 0 to 76.6. No growth index was calculated for individual tagged culms.

For each clump in each year (centred on the wet or dry season as relevant), three measures of canopy retention were derived: the number of months in full leaf, the number of months of leaflessness, and the lowest canopy-fullness level achieved. A clump was considered to be in full leaf if its canopy fullness was more than 75 percent, and leafless if its canopy fullness was less than 2 percent. Numbers of months were converted to proportions of the year, and all measures subject to the arcsine transformation (Zar 1984) prior to analysis. Two-way ANOVAs with site as a factor and year as a repeated measure were performed in the General Linear Model module of Statistica (StatSoft Inc. 1984-2002).

The number of culms reaching class C provides a good measure of annual culm recruitment. The total for a site/year was used as a base for calculation of the relative abundance of each size class in each month. "Overproduction" and subsequent loss of culm shoots during the early stages of development means that the measure of relative abundance may exceed 100 percent. For each assessment of tagged culms, the proportion that had incremented a branch class since the previous assessment was calculated and attributed to the mid-point between assessments. Leaf shoot scores for tagged culms were converted to the mid-range of their class, and the site mean calculated.

Rainfall data were obtained from the Commonwealth Bureau of Meteorology for the Annaburroo AWS rain station, which is directly between the riparian and hill sites, and for the Wildman Rangers rain station which is 28 km from the riparian sites and 22 km from the hill site with no nearby hills greater than 150 m above sea level. Rainfall records from Annaburroo AWS were used preferentially in analysis but were missing for much of both dry seasons and also for the first half of the 2001/02 wet season. Significant dry season rainfall events were corroborated with local observations by the Ostwald family at Mary River Park and rainfall observations available on-line at the Commonwealth Bureau of Meteorology's web-site *http://www.bom.gov.au* at the time.

Results

Environmental rhythms and perturbations

The wet season preceding the study (2000/01) was 27 percent above the estimated average rainfall. The 2001/02 wet season began in late September and rain was consistent thereafter until early April, the total being 9 percent below average. The 2002/03 season commenced with light showers in late September, was followed by consistent rain only from early November, finished abruptly in early March, and was 23 percent below average. An uncharacteristic dry season rainfall event of 66 mm (confirmed at Annaburroo AWS) occurred on 2 June 2003, with a further c. 25 mm falling on 6 September. The 2003/04 wet season commenced in early November. Rainfall data for the study period are summarised beneath phenological observations in Figures 1 & 2.

At the hill site, no clump was inundated by floodwaters. All upper riparian clumps were either inundated or within 5 m of floodwater briefly in each of the two wet seasons, but not necessarily at the time of a formal assessment, and none was recorded as being within 5 m of floodwater for more than one month in each wet season. The base of eight lower riparian clumps were at least partly under water for one month in each wet season, one clump was under water for two months in each wet season and one for four and six months respectively. Lower riparian clumps remained within 5 m of surface water for a mean of 5.9 months in the 2001/02 season and 6.0 months in 2002/03, with a range of 2–12 and 1–12 months respectively.

All clumps at the upper and lower riparian sites were burnt by wildfire on 16 August 2001. Canopy damage was generally light but varied from nil to 100 percent, but most clumps suffered substantial culm mortality as a result of heat-scorching of culm bases (Franklin unpubl. data). However, all clumps survived, and with the onset of rains six weeks later, the canopy of all but two regenerated vigorously. No fire or other canopy disturbance was noted at the hill site, but one clump became progressively and markedly unhealthy as the study progressed. Almost all newly-emerged culm shoots at the hill site were destroyed by feral pigs (*Sus scrofa*) in December 2001, whereas damage by pigs was negligible at the riparian sites in both years and light at the hill site in 2002.

Canopy phenology

Bambusa arnhemica clumps were variously totally deciduous, partly deciduous, or in a few lower riparian clumps, quite evergreen during the dry season (Fig. 1). There were significant differences between sites but not years in three measures of canopy retention (Table 1). Post-hoc tests Tukey HSD tests identified significant ($P < 0.05$) differences between all sites for all three parameters. There was a consistent gradient of: lower riparian – upper riparian – hill, the lower riparian site remaining in full foliage for the longest period, having the shortest period of leaflessness (zero in all clumps), and retaining the most foliage during the dry season. The significant interaction between site and year for the number of leafless months occurred because clumps remained leafless longer in 2003 than 2002 at the upper riparian site (Tukey HSD, $P = 0.017$) but there was no significant difference between years at the other sites (lower riparian, $P = 1.0$; hill, $P = 0.81$).

A major flush of leafy shoots (Growth Index [GI] > 40) occurred over a one to three month period after the beginning of the wet season (Fig. 1). At the riparian sites in 2001, leaf shoot commenced shortly prior to the first showers and was particularly prolonged, but in 2002 commenced shortly after the first showers and peaked over a shorter period. At the hill site, leaf shoot commenced some time (*c.* 1 month) after the first showers in all three years. In both available years, a second minor peak occurred in April or May at all sites (consisting largely but not entirely of foliation of new recruits; see below), but this peak was much more obvious at the two riparian sites (GI 6–25) than the hill site (GI 4.0 and 2.6). Unseasonal heavy rain in early June 2003 was followed by another small peak (GI < 10) at the upper riparian and hill sites, but was not evident at the lower riparian site, whereas the two riparian sites achieved GI > 20 following the September fall but no response was evidence at the hill site.

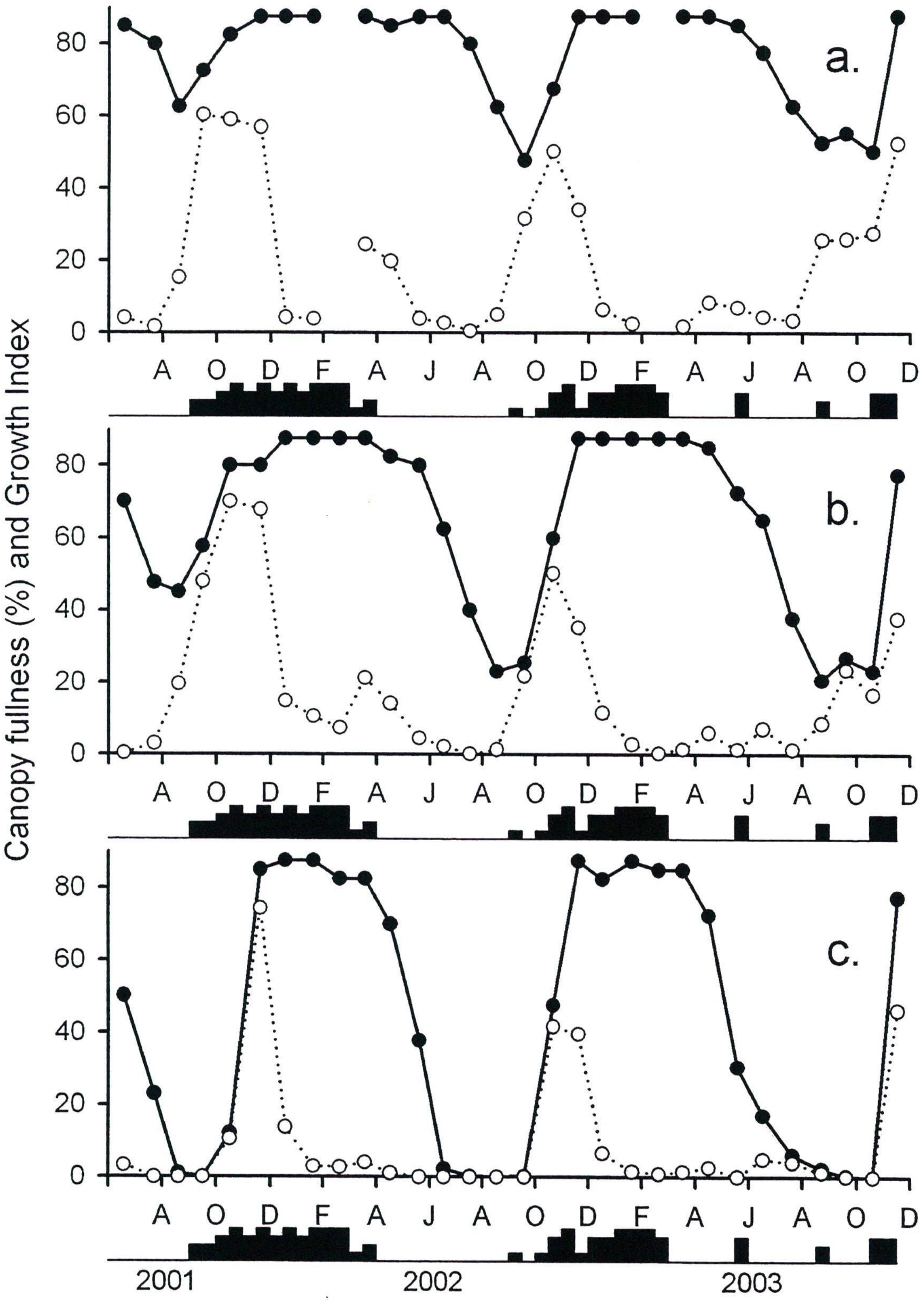

Figure 1. Canopy fullness (solid line) and Growth Index (dotted line) for *Bambusa arnhemica* at three sites: *a.* lower riparian, *b.* upper riparian, and *c.* hill.

The x-axis ticks indicate the centre of the stated month. The small bar charts below the month labels (identical below each graph) indicate 4 categories of half-month rainfall totals: 10–25 mm; 25–50 mm; 50–100 mm; and > 100 mm.

Table 1. Site and year effects on canopy retention in *Bambusa arnhemica*. Analyses are two-way ANOVAs with site as a factor and year as a repeated measure.

Data have been arcsine transformed prior to analysis. The differences are illustrated in Figure 1 and post-hoc Tukey HSD tests reported in the *Results*.

Parameter	Effect	*F*	d.f.	*P*
months of full canopy	site	16.4	2,27	< 0.001
	year	2.1	1,27	0.16
	site * year	1.7	2,27	0.21
months leafless	site	86.6	2,27	< 0.001
	year	1.7	1,27	0.20
	site * year	6.1	2,27	0.007
lowest canopy fullness	site	27.1	2,27	< 0.001
	year	0.2	1,27	0.64
	site * year	0.1	2,27	0.92

Culm shoot phenology

New culm shoots (class A, Fig. 2) began to emerge after the onset of consistent rains early in the wet season, peaking in abundance one to two months later. Emergence began earlier relative to rainfall at the two riparian sites in 2001 than in other years and at the hill site. The double-peak in class A shoots at the hill site in 2001/02 (Fig. 2c) was evidently a response to the near complete annihilation of the first cohort by feral pigs. The major phase of elongation occurred in the mid- to late-wet season (the transition to classes B & C in Fig. 2; see also Fig. 3). Culms tagged in April had all either already completed elongation (the two riparian sites in both years) or had ceased elongation prematurely. Of six tagged culms at the hill site in 2002, only two had elongated fully, the remainder achieving an estimated 5, 70, 90 and 90 percent of their potential length, whereas in 2003 six of eight had elongated fully, the remainder achieving 90 and 95 percent of their potential. The culm shoot that reached only 5 percent of its potential regressed and died during the dry season, whereas the remainder survived but their tips were clearly dead and they failed to resume elongation with the onset of the following wet season's rains.

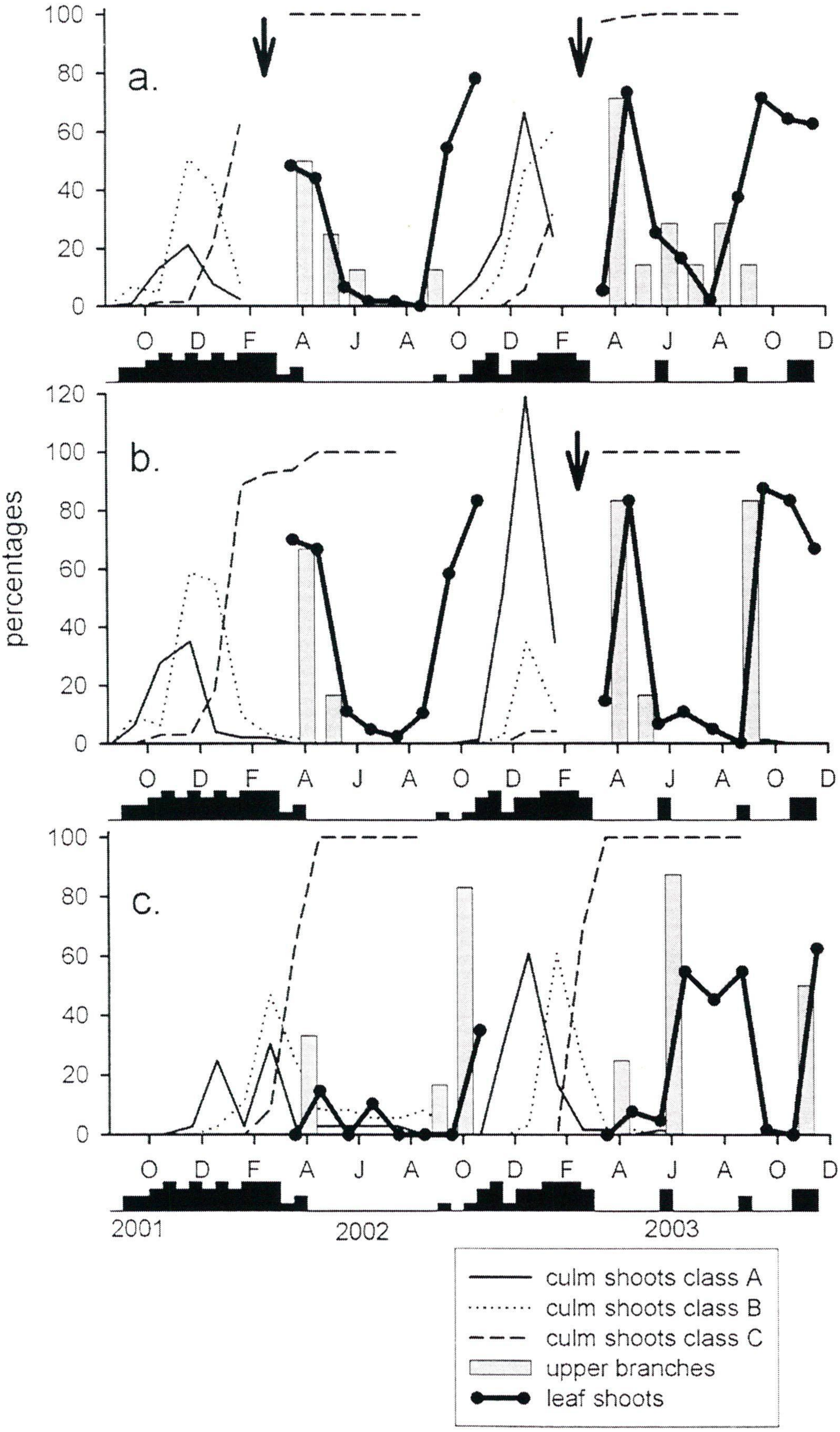

Figure 2. caption on next page

Figure 2 (on previous page). **Culm, branch and leaf growth of two annual cohorts of first year culms of *Bambusa arnhemica* at three sites: *a.* lower riparian, *b.* upper riparian, and *c.* hill.**
The number of culm shoots in each class is expressed as a percentage of the recruits (Class C) for the season. Upper branch growth is the percentage of culms that incremented a branch state class. Leaf shoots are the mean percentage of leafy shoots with unexpanded tips. See *Methods* for more detail. The arrows indicate missing culm counts due to monsoonal flooding. The x-axis ticks indicate the centre of the stated month. The small bar charts below the month labels (identical below each graph) indicate 4 categories of half-month rainfall totals: 10–25 mm; 25–50 mm; 50–100 mm; and > 100 mm.

After emergence, culm elongation rates remained below 5 cm per day for up to three weeks before increasing progressively to peaks of 15–25+ cm per day at mid-heights (Fig. 3), beyond which measurements were not obtained. The most rapid growth recorded was 2.06 m in 7 days 4 hours, a mean rate of 28.7 cm/day. The 2002/03 wet season began with only intermittent heavy rain. A nine-day spell at the end of the December in which only 14.2 mm was recorded was followed by a sharp but temporary decay in growth rates in early January 2003.

Branch and foliage development on first year culms is contingent on the previous stage of development and thus the observed patterns are less clear-cut. Primary branches were not leaf shoots, but secondary branches often were. Primary basal and upper branches began to emerge after or very shortly before the completion of elongation. Branch development, including that of leaf shoots, was concentrated in the late wet/early dry season, resuming rapidly by initiation of new branch shoots with the onset of rain in the following wet season. However, there was some growth through much the dry season, particularly at the lower riparian site (Fig. 2*a*). New culms at the hill site commenced/resumed branch/leaf shoot growth following unseasonal rainfall in June 2003, growth ceasing (and all foliage and branch tips drying off) before the onset of the main rains of the 2003/04 wet season (Fig. 2*c*), but this resumption and cessation of growth was not or only slightly evident at the riparian sites. Culms that had not fully elongated, and a few that had, did not commence branching and foliage development until the onset of the following wet season's (or unseasonal dry season's) rain.

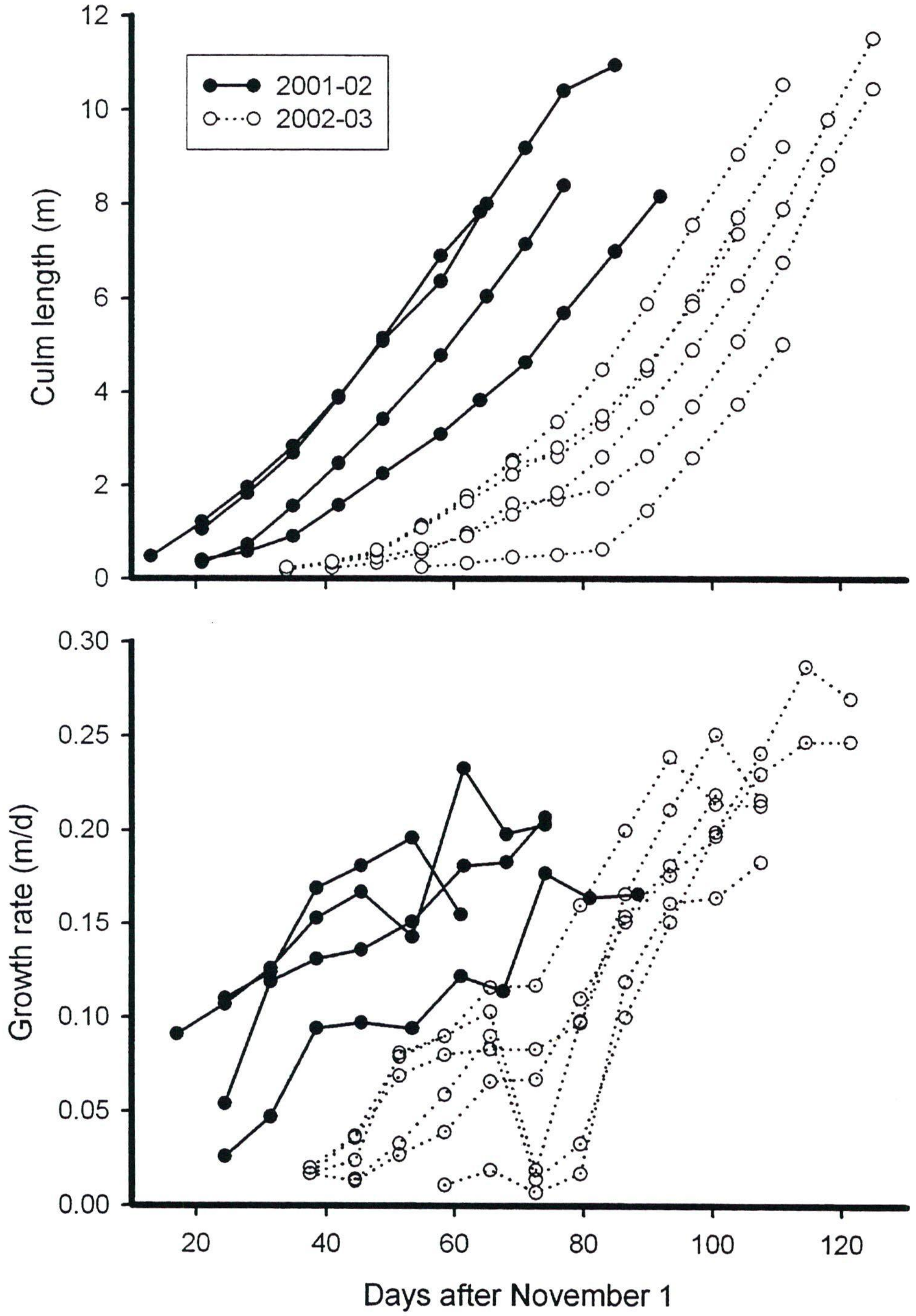

Figure 3. Length of culms over time and rates of elongation in the Top End Bamboo *Bambusa arnhemica*.

Discussion

The annual cycle in B. arnhemica

Most growth in *B. arnhemica* occurred in the wet season. During this time, the major leaf flush and culm elongation phenophases were undertaken in rapid succession and with limited overlap. Some leaf flush and branch development occurred in the late wet/early dry, more so at the riparian than hill sites and mainly on culm recruits that had completed elongation. Leaf drop commenced early in the dry season at the hill site and in the mid- to late-dry season at the riparian sites. Culm recruits and older culms achieved synchrony with leaf shoot at the onset of the following season's rains.

Leaf flush occurred promptly after seasonal, and sometimes unseasonal, rain in most site/year combinations, but shortly before the first wet-season rain at the two riparian sites in 2001. The latter was associated with the early emergence of culm shoots, and is thought to have been a response to the fire of August 2001. In that year, early culm shoots were of small diameter and arose from the rhizomes of culms damaged or killed by the fire, whereas later culm shoots were of normal size and arose from undamaged ramets (Franklin unpubl. data.). Rainfall of less than 25 mm appears to have been sufficient to trigger leaf flush at the riparian sites, but heavier falls may have been required at the hill site. However, the unseasonal rain of June 2003 produced the converse effect, for which one possible explanation is that the retention of canopy may inhibit "inappropriate" dry season leaf shoot. The apparent failure of such controls at the hill site may indicate incomplete adaptation to the monsoonal system, perhaps reflecting relatively recent colonisation by bamboo of north-western Australia from Asia (Franklin 2003*a*). The monsoon weather system in northern Australia has probably been in place since the Miocene, and there are numerous examples of highly-adapted flora and fauna (Bowman 2002). However, collection of data over a longer period is required to conclusively tease out time-of-year, rainfall and site effects on leaf flush.

The major commitment to culm elongation occurred in the mid-to late-wet season when moisture levels are most reliably high and clumps may be subject to prolonged inundation. An unusual dry spell in the poor wet season of 2002/03 is assumed responsible for a temporary but marked reduction in elongation rates similar to that documented in detail for Sri Lankan bamboos by Lock (1904). However, the elongation process appears not to have been adversely affected by inundation. It is possible that oxygen stored in internode cavities or obtained from aerial roots at culm nodes permits the species to function as a facultative aquatic (Cowie *et al.* 2000), though *B. arnhemica* appears intolerant of extended waterlogging during the dry season (Franklin & Bowman unpubl. data). In contrast, trees of Amazonian floodplain forests ceased growth and shed some or all leaves when flooded (Schongart *et al.* 2002).

If the major phenophases, and in particular the substantial commitment to culm elongation, are to be completed in the course of a wet season, culm elongation must be rapid, as indeed it was. An 18 m culm requires an average elongation rate of 16.1 cm/day to elongate in 16 weeks. Culm elongation rates in bamboo are classically sigmoidal with the peak rate occurring at close to half the final length (Porterfield 1928, Lodhiyal *et al.* 1998, Londono 1998), so it is likely that maximum rates of 20–30 cm per day documented for *B. arnhemica* represent the true peak. Such dramatic rates are not unusual amongst bamboos (Lock 1904, Kondas 1982, Shanmughavel & Francis 1996, Zhou BenZhi 1999, Lee & Addis 2001), but fall well short of the record 121 cm in a day reported for a Japanese bamboo culm shoot by Ueda (1960).

Tolerance of seasonal drought

The edaphic (flood) gradient along which the three sites were distributed yielded corresponding gradients in the period of full canopy retention, the extent of dry season canopy loss, the period of total canopy loss, the degree of development achieved by culm recruits during their first year, and also though less clearly in leaf flush/rainfall relations. In all cases, clumps at the lower riparian site achieved the most favourable outcomes, and those on the hill site the least favourable. It is unclear to what extent the differences are attributable to the moisture provided by floodwaters, to the residual surface water in the billabong during the dry season, or to soil moisture retention capacity and soil fertility. Divakara *et al.* (2001) found bamboo roots up to 9.6 m from the base of large clumps, so it is possible that many clumps of *B. arnhemica* at the lower riparian site retained access to free water for much of the dry season.

Bambusa arnhemica is facultatively deciduous, exhibiting almost the full range of canopy retention and leaf flush patterns documented amongst nearby savanna trees by Williams *et al.* (1997), ranging from evergreen to fully deciduous for up to four months during the dry season. In being facultatively deciduous, *B. arnhemica* differs from many deciduous trees of the wet-dry tropics, in which leaf drop appears obligate (Eamus & Prior 2001; but see Borchert *et al.* 2002). Myers *et al.* (1998) found that one of two deciduous tree species exhibited a response to irrigation, retaining foliage for longer and refoliating earlier, but both species nevertheless remained fully deciduous. Facultative deciduousness may, however, be a common characteristic of bamboos (Troup 1921, Fanshawe 1972).

Progressive stem damage from branch tips as a result of hydraulic failure is another form of drought response (Rood *et al.* 2000, Vesk & Westoby 2003). The tips of culms that failed to elongate before the onset of the dry season died, as did the tips of branches that flushed at the hill site in June 2003 but failed to complete elongation. Tip die-back was also observed on "normal" growth axes, most obviously at the hill site (pers. obs.), and may be a commonplace dry-season event. The consequences of branch die-back may not be great, as the unrestricted monoclade growth form of *Bambusa*, in which many branches may be produced successively from each node (McClure 1966, Franklin 2003*b*), provides opportunity for replacement and gap-filling. However, the consequences of incomplete elongation of culms may be severe because of failure to reach the canopy, to which high light levels are restricted during the wet season. Observations suggest that, even where a branch subsequently takes on the role of leading shoot, its diameter, height and foliage capacity never approach that of an undamaged culm. The observed failures of culm elongation at the hill site, whether due to delays induced by predation of culm shoots or to the shorter period over which moisture is abundant, suggest limited capacity at that site to cope with environmental stresses. It could go some way towards explaining why *B. arnhemica* is abundant along watercourses but infrequent on hillsides (Franklin & Bowman 2003).

Conclusion

The bamboo growth form contrasts markedly with that of dicotyledonous trees. The facultative nature of its deciduousness and perhaps also leaf flush, along with the highly flexible branching process in *Bambusa*, provides an ability to both cope with and exploit the unpredictable elements of a monsoonal system. On the other hand, culm elongation is a critical phenophase which must be completed in a single growing season. The intensity of the monsoonal system provides a predictable opportunity for exceptional rates of culm elongation, but the severity of the dry season may constrain the process, and thus the occurrence of bamboos, to sites with high rainfall and/or high soil moisture retention.

Acknowledgements

This project was supported by Parks & Wildlife (Northern Territory) and the Key Centre for Tropical Wildlife Management. I am grateful to the Ostwald family of Mary River Park for access and support with the Mary River sites, and to Tony Freshwater for permission to work on Annaburroo Station. Mike Ostwald took culm length measurements for me during several absences. Nigel Mules and Melissa Fitzgerald from the Commonwealth Bureau of Meteorology provided rainfall data. David Bowman, Lynda Prior, Peter Whitehead and Robert Taylor provided helpful comments on a draft of this manuscript.

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Chapter 7:

Synthesis and conclusions

Taxonomy and biogeography

Based on its current distribution, and the distribution of bamboo diversity in the Australian and Asian region, it seems reasonable to assume that *Bambusa arnhemica* or its predecessor arrived in northern Australia from mainland Asia or the Indonesian archipelago at some time in the past, and that that time is neither particularly recent nor very ancient. Though *B. arnhemica* may be related to either or both of the two widespread Asian thorny *Bambusa* bamboos (*B. bambos* and *B. blumeana*), the morphological description provided in Chapter 2 clarifies that it is quite distinct from them. Furthermore, it is now possible with greater clarity to confirm the assertion of Muller (1997) that *B. arnhemica* is not close to either of the other mainland Australian woody bamboos (Table 1). Whereas *B. arnhemica* is a moderately large and erect, thick-walled and thorny bamboo with complex branching and small leaves, *Neololeba atra* is a thornless, thin-walled and slender-culmed species somewhat reliant on support from nearby plants, and has a simple branching system with a few large leaves. *Bambusa moreheadiana* differs even more radically, having long, slender, scandent culms that give rise distally to new culms (Muller 2001). Substantial differences in floret and inflorescence structures appear also to exist, but considerably more information and specialist analysis is needed to confirm their significance.

Nevertheless, the lack of direct evidence that *B. arnhemica* is other than a recent arrival to northern Australia is slightly disconcerting. Two avenues of research may provide more tangible evidence. The first, alluded to in the Introduction, is that anthropologists could examine Aboriginal stone tools for evidence of bamboo residues. The second is a series of genetic analyses being currently undertaken by Prof. Yuji Isagi, Prof. Hiromi Tsubota and myself. Population genetic analyses began against the background of allochronic isolation of flowering patches, but may now be placed in the wider context of colonisation, dispersal and rates and direction of gene flow. Taxon-level analysis involving all three mainland Australian bamboos and a selection of thorny and non-thorny Asian *Bambusa* species may shed light on the origin and level of distinctness of *B. arnhemica*.

Table 1: Comparison of selected traits of the three mainland Australian bamboos.

Characteristics of *Bambusa arnhemica* are based on Chapter 2 of this thesis, *Neololeba atra* on Holttum (1967, as *B. forbesii*) and Widjaja (1997), and *B. moreheadiana* on Clifford (1993) and Muller (2001). Note that, as was the case with *B. arnhemica* prior to my description, there are inadequacies and discrepancies in the descriptions of *N. atra* and *B. moreheadiana*, so that the information provided about these species should not be regarded as authoritative.

Trait	*B. arnhemica*	*N. atra*	*B. moreheadiana*
Habit	clumping	clumping	scandent
Height (culm length)	10-20 m	8–12 m	? to more than 50 m
Culm diameter	to 8 (–13) cm	to 4 cm	to 4 cm
Internode length	to 30 (–43) cm	30–80 cm	to 30 cm
Culm branching position	mostly basal and upper	upper only	??
Culm branch numbers	often >>3 per node	1–3 per node	mostly 1 per node
Orders of branching	to 4 (–5)	two	? to 2
Culm sheaths blade	*c.* 30–40 x 15 cm	to 18.5 x 6.5 cm	? to 12 x 8 cm
Culm sheath auricles	almost absent	prominent	reduced
Leaves	5–20 x 0.8–3.0 cm	30–55 x 5–9.5 cm	to 30 x 5 cm
Pseudospikelet length	to 45 (–70) mm	to 20 mm long	5–6 mm
No. florets per pseudospikelet	to 16 (mostly >> 6)	7–12	3–4
Lodicules	usually 3 per floret	absent	sometimes present, small
Flowering	strictly semelparous	?iteroparous	??? (infrequent)

Life history implications

The remarkable life history strategy of gregariously semelparous bamboo is potentially fertile ground for research and the development of ideas relating to the adaptive value and evolution of life histories. Its particular potential lies in clarifying the as yet fuzzy line between generally untenable notions of group selection, occasionally tenable notions of neighbourhood selection (Wilson 1987), and well-supported ideas about kin and individual selection. Several possibilities have been alluded to in this thesis.

Gregariousness in bamboos appears unusual in that it has both spatial and temporal components, the spatial in the patchy occupation of environments, and the temporal in infrequent but synchronous flowering. However, quantitative evidence supporting and explaining the adaptive value of gregariousness in bamboos is scant; indeed, it is so scant that a skeptic could easily argue that no case exists for it being other than accidental.

Management implications

Bambusa arnhemica is confirmed as a native species endemic to the Top End of the Northern Territory. As such, it warrants adequate levels of protection including careful consideration of the sustainability of any commercial harvest from wild stands. Harvest issues will be taken up in considerable detail in subsequent work. However, several issues are worth highlighting at this point, either because they are readily apparent from the work already presented, or because they are sufficiently general in nature, clear from general observation, and important.

Bambusa arnhemica is well-represented in conservation reserves, with extensive riparian stands in Kakadu National Park (map in Chapter 3) and the proposed Mary River National Park, and smaller stands in at least the Black Jungle Conservation Reserve, Litchfield National Park and Djukbinj National Park. A major set of non-riparian stands including several of the most extensive occur in the proposed Mary River National Park, there are at least two non-riparian stands in Kakadu National Park, two in the Shady Camp Conservation Reserve, and very small stands (both less than 10 clumps) in Charles Darwin National Park and the Duke Street Rainforest. However, there is little if any reservation of stands in the Daly River catchment, and poor reservation of stands around Darwin Harbour. In Darwin Harbour, only the Talc Head stand remains substantial, a number of stands having suffered seriously in the face of development and human antipathy, and others from suppression of seedlings by weeds following mass-flowering in 1996. Stands on Aboriginal land on Melville Island may be regarded as satisfactorily reserved, but are suffering from considerable damage by Buffalo (*Bubalis bubalis*).

Non-riparian stands of *B. arnhemica* are infrequent and small. Evidence presented in Chapter 6 suggests that they may be at the limits of the species' environmental tolerance and thus less able to cope with harvest or other adverse influences. Although not generally exposed to harvest, I have seen evidence, in the form of cut rhizomes, of illegal harvest activity in stands in the Shady Camp Conservation Reserve. Given this combination of scarcity and apparent vulnerability, I recommend that commercial harvest be totally excluded from non-riparian *B. arnhemica* stands.

There is no doubt that fire plays a major role in determining where *B. arnhemica* occurs. Although general observation and the data in Chapter 4 suggests that savanna fires often stop at the edge of *B. arnhemica* stands, fire can and does enter stands. I will subsequently present data that demonstrate substantial short-term consequences of an intense late dry-season fire, consequences which if repeated with some frequency might be anticipated to have serious consequences for stand health. Feral pigs (*Sus scrofa*) also negatively affect culm recruitment (Chapter 6 and unpubl. data). Fire and pigs may thus effectively "compete" with humans for any excess of culm shoots that *B. arnhemica* may yield, and commercial development of *B. arnhemica* resources may require these issues to be addressed pre-emptively.

The unique life form and life history of bamboos creates an unusual challenge for management. Unlike most forestry trees or animals, harvest is not of unitary individuals, and conventional population models do not apply. However, nor is harvest simply analogous to the harvest of fruit. There may be some simple parallels with coppice systems, but even these neglect or underplay the demographic consequences of harvest on a clonal organism. For a leptomorph (running) bamboo under intensive management, Isagi *et al.* (1997) approached the problem as one of carbon cycling, in which the canopy is the productive engine to be optimized, the rhizomes are the storage system, and the culms the product and the physical support system. Conceptually, this model is most helpful, but it has major functional limitations for pachymorph (clumping) bamboos. Leptomorph bamboos tend to form evenly-spaced stands of culms superficially resembling a conventional forest, particularly so under intense management, permitting what is effectively a colonial density-dependant response to harvest. In contrast, a clumping bamboo has less options to optimize use of space, especially so as clumps are highly sectorised (unpublished data). This may be particularly problematic in a harvest system subject to only low-intensity management where peripheral shoots are much more likely to be harvested than those emerging at the centre of clumps (unpublished data). Furthermore, in the case of wild *B. arnhemica* stands, the objective of the management agency are unlikely to be simply or primarily to optimize production.

The gregarious flowering behaviour and subsequent death of stands renders the shoot resource unavailable for a period of perhaps ten years, but this period of unavailability is staggered chaotically across the landscape. This adds considerable complexity to the management of an annual resource, and creates the risk of periodic intensification of the harvest in areas that remain to flower. It is also possible that *extreme* over-harvest may reduce the ability of bamboo stands to dominate space and thus to ensure successful regeneration, particularly if peripheral shoots are harvested preferentially, thus reducing the rate of clump expansion and occupation of space.

Whilst clumping bamboos are ideal objects for horticulture, achieving sustainability in the absence of intensive management may not be easy.

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