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Frequency of Cyanogenesis in Tropical Rainforests of Far North Queensland, Australia

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• *Background and Aims* Plant cyanogenesis is the release of toxic cyanide from endogenous cyanide-containing compounds, typically cyanogenic glycosides. Despite a large body of phytochemical, taxonomic and ecological work on cyanogenic species, little is known of their frequency in natural plant communities. This study aimed to investigate the frequency of cyanogenesis in Australian tropical rainforests. Secondary aims were to quantify the cyanogenic glycoside content of tissues, to investigate intra-plant and intra-population variation in cyanogenic glycoside concentration and to appraise the potential chemotaxonomic significance of any findings in relation to the distribution of cyanogenesis in related taxa.
• *Methods* All species in six 200 m^2 plots at each of five sites across lowland, upland and highland tropical rainforest were screened for cyanogenesis using Feigl–Anger indicator papers. The concentrations of cyanogenic glycosides were accurately determined for all cyanogenic individuals.
• *Key Results* Over 400 species from 87 plant families were screened. Overall, 18 species (4·5 %) were cyanogenic, accounting for 7·3 % of total stem basal area. Cyanogenesis has not previously been reported for 17 of the 18 species, 13 of which are endemic to Australia. Several species belong to plant families or orders in which cyanogenesis has been little reported, if at all (e.g. Elaeocarpaceae, Myrsinaceae, Araliaceae and Lamiaceae). A number of species contained concentrations of cyanogenic glycosides among the highest ever reported for mature leaves—up to 5·2 mg CN g^{-1} d. wt, for example, in leaves of *Elaeocarpus sericopetalus.* There was significant variation in cyanogenic glycoside concentration within individuals; young leaves and reproductive tissues typically had higher cyanogen content. In addition, there was substantial variation in cyanogenic glycoside content within populations of single species.
• *Conclusions* This study expands the limited knowledge of the frequency of cyanogenesis in natural plant communities, includes novel reports of cyanogenesis among a range of taxa and characterizes patterns in intra-plant and intra-population variation of cyanogensis.

Key words: Australia, β-glycosidase, chemotaxonomy, cyanogenic glycoside, cyanogenesis, defence, hydrogen cyanide, polymorphism, Queensland, screening, secondary metabolite, tropical rainforest.

INTRODUCTION

Cyanogenesis is the ability to release toxic hydrogen cyanide (HCN) from endogenous cyanide-containing compounds. It has long been recognized in plants (Conn, 1991; Seigler, 1991), and has been recorded in ferns, fern-allies, gymnosperms, as well as monocotyledonous and dicotyledonous angiosperms from >550 genera and 130 plant families (Conn, 1981; Poulton, 1990; Jones, 1998). Cyanogenesis in plants requires the presence of either an unstable cyanohydrin, or of a stable cyanogen and its degradative enzymes (Seigler, 1991). While cyanolipids have been identified from a few taxa (Mikolajczak *et al*., 1970), cyanogenesis in plants most commonly results from the hydrolysis of cyanogenic glycosides (Conn, 1981). Autotoxicity in intact plants is prevented by the spatial separation—either at the subcellular or at the tissue level—of the cyanogenic glycoside and catabolic enzymes (Kojima *et al*., 1979; Selmar, 1993*a*; Poulton and Li, 1994; Zheng and Poulton, 1995; Hickel *et al*., 1996). The catabolism of cyanogenic glycosides is therefore initiated upon tissue disruption, due to mechanical damage or ingestion by herbivores, for example, which enables mixing of enzymes and cyanogenic substrate (Wajant *et al*., 1994; Patton *et al*., 1997).

Little is known about the frequency of cyanogenesis in natural plant communities. This is despite a large body of literature documenting cyanogenesis in >2650 species of angiosperms worldwide (Lechtenberg and Nahrstedt, 1999). Indeed, as many as 11 % of all plant species are predicted to be cyanogenic (Jones, 1998). Historically, much of the interest in cyanogenesis centred around recording toxic plants with the potential for stock and human poisoning, the high frequency of cyanogenesis among food plants (Jones, 1998), and the potential utility of cyanogenesis and the structure of specific cyanogens in elucidating phylogenetic relationships between taxa (e.g. Gibbs, 1974). As a consequence, much of what is known about the frequency of cyanogenesis comes from surveys of regional floras, or of specific taxonomic groups. There are a number of substantial chemotaxonomic works incorporating information on cyanogenesis (see Hegnauer, 1966, 1973, 1986, 1989, 1990; Gibbs, 1974), several smaller and more specific chemotaxonomic works (e.g. Tjon Sie Fat, 1978, 1979*b*; Spencer and Seigler, 1985; van Wyk and Whitehead, 1990; Seigler, 1994), including work on Australian *Acacia* spp. (Conn *et al*., 1985; Maslin *et al*., 1988), and numerous inventories of cyanogenic species (e.g. Rosenthaler, 1919; Seigler, 1976*a*, 1976*b*; Tjon Sie Fat, 1979*a*; Francisco and Pinotti, 2000). Several Australian researchers were active in

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the field early last century, reporting a number of cyanogenic species and the specific cyanogenic constituents involved (e.g. Petrie, 1912, 1913, 1914, 1920; Finnemore and Cox, 1928, 1929; Finnemore and Cooper, 1936, 1938). More than 700 species in the Queensland flora were screened by Smith and White (1918). Further phytochemical screening of the Queensland flora was conducted by Webb (1948, 1949); however, there was negligible testing among tropical taxa. Importantly, many of these records are based on qualitative tests performed using herbarium specimens, and tests of this kind using dried material are by no means conclusive. One further limitation of these data in terms of extrapolating to natural plant communities is that negative results were often not reported.

Tropical rainforests are of particular interest in the study of plant chemical defences. Elevated herbivore pressure in tropical environments is hypothesized to have favoured both a diverse array of defences and high levels of investment in chemical defence (Levin, 1976; Levin and York, 1978; Coley and Barone, 1996; Kursar and Coley, 2003). Indeed, in the field of plant secondary chemistry, the tropical rainforest has been the focus of intense interest in co-evolutionary relationships between plants and herbivores, and the extraordinary inter-specific and intra-plant variation in chemical defence strategies (Feeny, 1976; Levin, 1976; Coley *et al*., 1985; Coley and Kursar, 1996).

On the whole, community-level studies of the distribution of chemical defences have focused on a small set of Asian and African rainforests (McKey *et al*., 1978; Gartlan *et al*., 1980; Davies *et al*., 1988; Waterman *et al*., 1988). In addition, these and other studies have tended to focus on C-based 'quantitative' defences (e.g. Coley, 1983, 1988). Among N-based defences, the greater awareness of the frequency of alkaloid-bearing plants in tropical and other ecosystems is a consequence of extensive phytochemical screening for bioactive compounds (e.g. Swanholm *et al*., 1960; Hartley *et al*., 1973; Smolenski *et al*., 1974; Collins *et al*., 1990; Hadi and Bremmer, 2001) or ecological research into specific plant–herbivore interactions (e.g. Janzen and Waterman, 1984; Hartmann *et al*., 1997), rather than systematic studies within natural communities (but see Mali and Borges, 2003).

There are some hypothesis-driven surveys for cyanogenesis. Two studies have investigated the frequency of cyanogenesis in floras, investigating evolutionary and ecological hypotheses about exposure to herbivory (see Kaplan *et al*., 1983; Adsersen *et al*., 1988; Adsersen and Adsersen, 1993). However, only the survey of Thomsen and Brimer (1997) in Costa Rican rainforest has been conducted in a systematic fashion, well defined with respect to forest area and plant size. As with other N-based defences, work on cyanogenic tropical rainforest species worldwide is limited, and there has been no work on cyanogenesis in Australian tropical rainforests, or any other form of chemical defence. The lack of work on cyanogenesis in diverse tropical rainforests is further surprising, as it is a readily detectable and constitutive chemical defence (Gleadow and Woodrow, 2000*b*).

Here we report some of the findings of a large-scale quantitative survey for cyanogenesis in Australian tropical rainforests. First, we investigated the frequency of cyanogenesis and the contribution of cyanogenic species to biomass (basal area) in lowland, upland and highland tropical rainforest in north Queensland, Australia. Conducting the survey in a standardized fashion will enable comparison with other communities (e.g. Thomsen and Brimer, 1997). Secondly, intra-plant and intra-population variation in concentrations of cyanogenic glycosides was quantified. The high level of endemism among the Australian tropical rainforest flora (Webb and Tracey, 1981) and the number of rainforest taxa previously untested for cyanogenesis underscore the potential for novel reports of cyanogenesis within different taxonomic groups. Finally, therefore, this study aimed to investigate the potential taxonomic significance of cyanogenesis reported here. Overall, this study aimed to expand the limited knowledge of the frequency of cyanogenesis in the Australian flora and in natural plant communities.

MATERIALS AND METHODS

Field sites

Field work was conducted between July 1999 and September 2002. Six 200 m^2 plots (20×10 m) were established at each of five sites (total area 1200 m^2 per site) in lowland and upland rainforest in the tropics of north east Queensland, Australia (Fig. 1). Six plots were selected for two reasons: first, the number of new species captured with each additional plot had reached a plateau at around five species and, secondly, it was a realistic sample size given the time and resources available. Sites were selected to capture maximum species diversity as on the Atherton Tablelands, forest type and species composition vary both with substrate and with altitude (Tracey, 1982). Further, to enable comparison of forests occurring on different soil types, two pairs of sites with similar altitude and rainfall were selected. The first pair comprised a site on soil derived from basalt at Lamins Hill and one on soil derived from granite at Mt Nomico (Fig. 1). The second pair comprised sites on soils derived from basalt and rhyolite at Longlands Gap (Fig. 1). A fifth site in lowland rainforest near Cape Tribulation and Myall Creek, on soil derived from metamorphic substrate, was also surveyed (Fig. 1). The distribution of cyanogenic species in relation to resource availability (soil nutrients) will be addressed elsewhere (see Miller, 2004).

It was not possible to control strictly for logging history; all sites on the Atherton Tablelands had been selectively logged prior to the declaration of the Wet Tropics World Heritage Area in 1988. Detailed site descriptions are provided in Miller (2004).

All individuals (palms, trees and vines) with a diameter at breast height (dbh) of $\geqslant 5$ cm were tagged and identified. All additional species (dbh <5 cm) present in lower strata, with the exception of herbaceous ground species, were also tagged and identified.

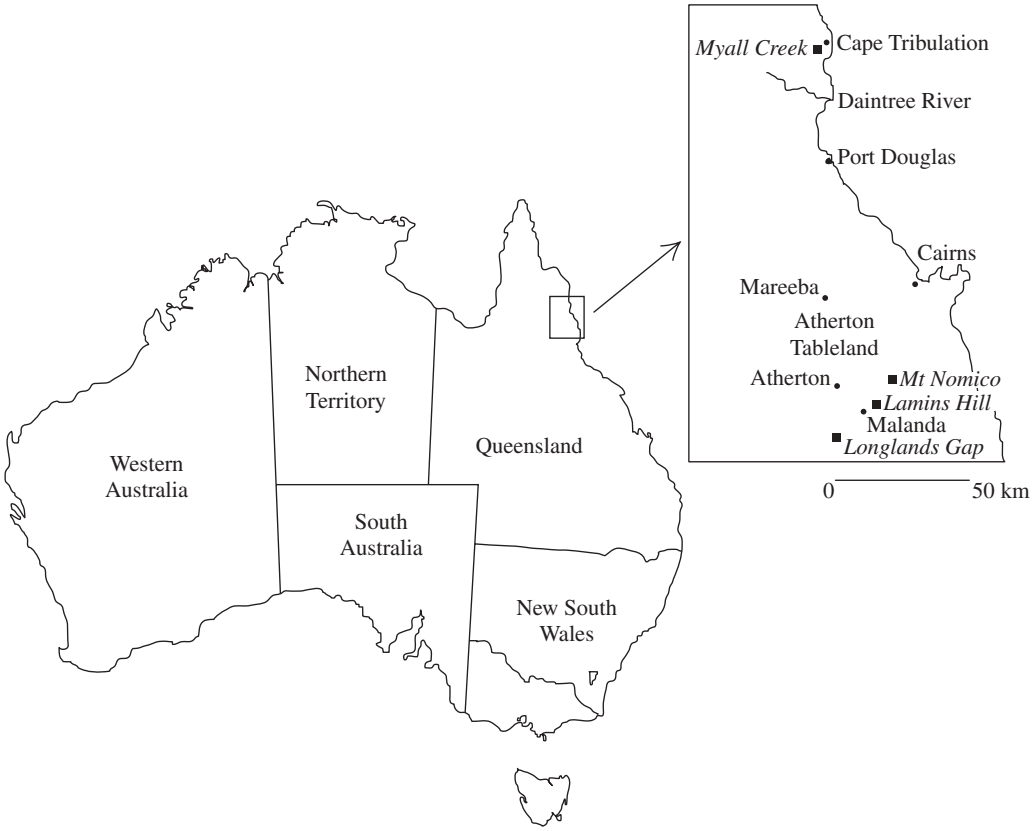

FIG. 1. Location of study sites in tropical rainforest in far north east Queensland, Australia. There were two pairs of sites in upland rainforest on the Atherton Tableland: Lamins Hill (17°22·4′S, 145°42·5′E) and Mt Nomico (17°13·3′S, 145°40·4′E), and two sites at Longlands Gap (17°27′S, 145°28′E). A fifth site was in lowland rainforest near Myall Creek and Cape Tribulation (16°06·2′S, 145°26·9′E).

Samples of all cyanogenic species, as well as species dominant at each site, and some rare species were pressed and lodged at the University of Melbourne (MELU) and Brisbane (BRI) Herbaria. Accession numbers, where assigned, are listed (Appendix).

Climate

The climate in far north Queensland is characterized by a marked wet season from December to April. Climate recording stations in the study area are scattered, therefore data specific to each site were not available. While located in the tropical latitudes, because of its higher altitude, the climate of the Atherton Tableland is semi-tropical. Mean annual temperature within the study area on the Tableland is 22 °C (Nix, 1991), with a minimum of 10 °C (Hall *et al*., 1981; see Graham *et al*., 1995). All the upland and highland rainforests surveyed on the Atherton Tableland have high average annual rainfall, generally in the range 2000–3000 mm plus cloud interception (Tracey, 1982). For example, the average annual rainfall at Lamins Hill is 3584 mm, based on 30 years of records from the Queensland Bureau of Meteorology (see Osunkoya *et al*., 1993). In contrast, the climate in the coastal lowland tropical rainforest near Cape Tribulation is characterized by higher temperatures. Mean daily temperatures range from 28 °C in January to 22 °C in July, and temperatures may reach the mid to high 30 s during the summer months. Average annual rainfall is also high, at 3928 mm recorded at Cape Tribulation (based on 65 years of records from the Queensland Bureau of Meteorology).

Sites

Upland and highland rainforest. The upland rainforest at Lamins Hill [17°22·4′S, 145°42·5′E; altitude 850 m above sea level (a.s.l.); Fig. 1] is classified as complex mesophyll vine forest on basalt (type 1b; Tracey, 1982; Tracey and Webb, 1975). This forest type typically occurs on upland sites (400–800 m), on high fertility kraznozem soils derived from basalt, with high rainfall (Tracey, 1982). It is characterized by a closed canopy with multiple tree layers, and an uneven canopy with height ranging from 35 to 45 m (Tracey 1982).

The upland rainforest at Mt Nomico (17°13·3′S, 145°40·4′E, 900 m a.s.l.; Fig. 1) is within the Gillies Range State Forest, and is on low nutrient soil derived from granite. The forest is classified as complex notophyll vine forest, typical of upland granitic soils (type 6; Tracey, 1982; Tracey and Webb, 1975).

In the highland rainforest of Longlands Gap State Forest (altitude 1100–1200 m a.s.l.), there is a sharp boundary in forest type defined by basalt (17°27·7′S; 145°28·5′E) and rhyolite (17°27·3′S, 14528·6′E) parent substrates.

On basalt, the forest is complex notophyll vine forest (type 5a; Tracey, 1982; Tracey and Webb, 1975), a forest type characterized by an uneven canopy (20–40 m high) and numerous tree layers, typical of basaltic cool wet uplands and highlands (Tracey, 1982). On rhyolite, the forest is simple microphyll vine forest (type 9; Tracey, 1982), which is common on upland granitic soils (800–1300 m), and is characterized by an uneven canopy 20–25 m high, with emergent *Agathis atropurpurea* (up to 35 m).

Lowland rainforest. The fifth site was in lowland rainforest in the Daintree World Heritage Area, near Cape Tribulation (Fig. 1). The site was near to Thompson and Myall Creeks (16°06·2′S, 145°26·9′E; altitude 40 m a.s.l.). The forest is complex mesophyll vine forest (type 1a; Tracey, 1982), the canopy is irregular, from 25 to 33 m in height, and supports a great diversity of species and life forms, including many palms and lianas. The floristic composition is patchy, with considerable variation in canopy and understorey dominants over small distances (Webb *et al*., 1972; Tracey, 1982). The soil is relatively nutrient-poor red clay loam podsol derived from metamorphic substrate.

Sampling for detection of cyanogenesis

Whole leaf samples (1–2 g f. wt) were taken from individuals with a dbh $\geqslant$5 cm, and from all additional species in the lower strata, until at least three individuals of each species had been sampled. Where possible, the youngest fully expanded leaves without epiphyllous communities were selected; however, in the case of samples acquired by pruning shears attached to extension poles or by slingshot and rope from the canopy, it was not always possible to be selective. In instances where it was not possible to obtain samples from large canopy trees, samples were taken from nearby individuals of the same species. Fresh whole leaf samples used for cyanide testing were stored in air-tight bags on ice until tested for cyanide 2–6 h later using Feigl–Anger (FA) papers (Feigl and Anger, 1966). Individuals of rare species, and those with little foliage, were sampled only once for analysis in the laboratory where a quantitative assay was used to test for cyanogenesis using freeze-dried ground tissue. Because cyanogenesis is known to be a polymorphic trait (e.g. Hughes, 1991; Aikman *et al*., 1996), a minimum of three individuals of all species was tested, more where species were common. Owing to the diverse and heterogeneous nature of the forests, multiple individuals of each species were not always represented in the plots. Therefore, for these rare species, testing individuals located outside the plots was required, and still there were several species for which only single samples were obtained.

A range of other factors was taken into consideration when sampling. For example, given that young leaves of tropical species, in particular, are typically more highly defended than older leaves (Coley, 1983; Coley and Barone, 1996), both young (soft expanding leaves) and old (recent fully expanded) leaves were tested for cyanogenesis, where possible. In addition, depending on availability, fruit and flowers from several species were tested. Owing to the large number of species and samples in the survey, it was not possible to examine seasonal trends in defence; however, individuals of the majority of species were tested in wet and dry seasons for qualitative changes in cyanogenic status, as there is some evidence for seasonal variation in cyanogenesis (Seigler, 1976*b*; Janzen *et al*., 1980; Kaplan *et al*., 1983). Finally, because edaphic factors have been reported to affect the expression of cyanogenesis (e.g. Urbanska, 1982), species found on more than one substrate type were tested at each site.

Sample collection, handling and storage for quantitative analysis

In addition to samples for fresh cyanide tests, whole leaf samples (again recent fully expanded leaves) were taken for quantification of cyanogenic glycosides. All individuals of species that produced a positive result and individuals of rare species were sampled. Depending on sampling conditions, samples were either placed immediately into liquid nitrogen, or placed in a sealed air-tight bag and kept on ice for 2–6 h until snap frozen in liquid nitrogen. Frozen samples were transported to the laboratory on dry ice, freeze-dried and stored on desiccant at −20 °C for analysis. Freeze-dried samples were ground using either a cooled IKA Labortechnic A10 Analytical Mill (Janke and Kunkel, Stanfen, Germany) or, for smaller samples, an Ultramat 2 Dental Grinder (Southern Dental Industries Ltd, Bayswater, Victoria, Australia).

Chemical analyses

Detection of cyanogenesis: Feigl–Anger papers. The presence of cyanogenic compounds in fresh field samples was determined using FA indicator papers (Feigl and Anger, 1966). FA papers were selected in preference to picrate papers because FA papers are more sensitive (Nahrstedt, 1980) and less prone to giving false-positive results (Brinker and Seigler, 1989). FA test papers were prepared according to Brinker and Seigler (1989). Because FA papers can be sensitive to moisture and light (Brinker and Seigler, 1989), they were stored in the dark and on desiccant until use.

Fresh leaves (approx. 1–2 g f. wt) were crushed in duplicate screw-top vials. Old and young foliage samples were tested separately. To facilitate cyanogenesis, 0·5 mL of water was added to one of the vials, and pectinase from *Rhizopus* spp. (Macerase® Pectinase, 441201 Calbiochem®, Calbiochem-Novabiochem Corp., La Jolla CA, USA) (0·4 g L^{-1}) in 0·1 M Tris–HCl (pH 6·8) was added to the other. Pectinase has been found to have non-specific β-glycosidase activity (Brimer *et al*., 1995) and, therefore, in the absence of sufficient endogenous β-glycosidase, enables tests for the presence of cyanogenic glycosides to be made. The indicator papers were suspended above the tissue by means of the screw-top lid, and vials were left at room temperature and checked after 12 and 24 h. This 24 h time period, used in other surveys (e.g. Dickenmann, 1982; Thomsen and Brimer, 1997; Buhrmester *et al*., 2000; Lewis and Zona, 2000), was selected to avoid spurious test results due to substantial bacterial contamination

which may occur beyond 24 h (Saupe *et al*., 1982). Tissue of known cyanogenic species, *Prunus turneriana* or *Ryparosa javanica*, was used as a positive control. Moderate to strongly cyanogenic samples gave a positive result within a few minutes or up to a few hours, while more weakly cyanogenic samples took several more hours. In accordance with the recommendations of Brinker and Seigler (1989), a new test was conducted for any samples producing a slow positive response (24 h) in case of interference by microbial cyanogenesis. In addition, any samples with inconclusive colour change were re-tested. An individual was considered cyanogenic if a positive, repeatable result was obtained, and a species was considered cyanogenic if at least one individual produced a consistent and repeatable positive result. A negative test result indicates the absence of a cyanogenic glycoside, or of the specific cyanogenic β-glycosidase, or both.

In the few instances where insufficient tissue was available for both FA paper tests using fresh leaves and subsequent laboratory analysis, cyanogenesis was determined based on the quantitative assay of freeze-dried ground leaf tissue (as described below) by comparison with a negative tissue control (e.g. *Alstonia scholaris* or *Aglaia meridionalis*).

In this study, tests for cyanogenesis used approx. 1–2 g f. wt of leaves, which is larger than tissue samples tested in previous surveys (e.g. 50 mg f. wt by Lewis and Zona, 2000; and 200 mg f. wt by Thomsen and Brimer, 1997; Buhrmester *et al*., 2000). According to Dickenmann (1982) who used 500 mg f. wt tissue, a weak positive reaction with FA papers, where part of the paper turns blue, indicated approx. 2–20 mg HCN kg^{-1} f. wt, while a strong reaction indicated >50 mg HCN kg^{-1} f. wt. These lower values equate to just over 6–60 μg HCN g^{-1} d. wt using a conversion based on the mean foliar water content of several species in this study, which was 70 %. In this study, based on fresh leaf tests and quantitative analysis of freeze-dried tissue from the same sample, the threshold sensitivity of FA papers was similar, within the range 5–8 μg HCN g^{-1} d. wt. This threshold sensitivity of FA papers corresponds well to the criteria of Adsersen *et al*. (1988) for classifying individuals as cyanogenic, where individuals with <93 nmol HCN g^{-1} f. wt (approximately equivalent to 8 μg HCN g^{-1} d. wt) were considered acyanogenic.

Polymorphism and confirmation of acyanogenesis

For the purposes of the survey, a species was considered cyanogenic if at least one individual produced a repeatable and positive test result. For a few species, not all individuals produced positive results using FA papers; therefore, some further investigation of the polymorphism for cyanogenesis in these species was conducted. First, to confirm the acyanogenic character of the individuals producing negative results with FA papers, a greater mass of freeze-dried tissue (100 mg) was assayed quantitatively for the evolution of cyanide (see below) and compared with a non-cyanogenic species, *A. scholaris*, as a control for baseline noise in the assay. Based on the criteria of Adsersen *et al*. (1988), if <8 μg HCN g^{-1} d. wt was detected, then that individual was considered acyanogenic.

Quantification of cyanogenic glycosides

The concentration of cyanogenic glycoside in plant tissues was measured by trapping the cyanide (CN), liberated following hydrolysis of the glycoside, in a well containing 1 M NaOH (Brinker and Seigler, 1989; Gleadow *et al*., 1998). Freeze-dried, ground plant tissue (30–50 mg) was incubated for 20–24 h at 37 °C with 1 mL of 0·1 M citrate–HCl (pH 5·5). Cyanide in the NaOH well was determined using the method of Gleadow and Woodrow (2002) adapted from Brinker and Seigler (1989) for use with a photometric microplate reader (Labsystems Multiskan® Ascent, with incubator, Labsystems, Helsinki, Finland). The method is highly sensitive; the determination of CN in NaOH is relatively specific for cyanide, and can detect as little as 5 μg L^{-1} (Brinker and Seigler, 1989). The absorbance was measured at 590 nm with NaCN as the standard.

RESULTS

Survey for cyanogenesis

In total, fresh leaf material from 401 woody plant species from 87 families was tested for cyanogenesis (Appendix). Cyanogenesis was found in 18 species from 13 families, representing 4·5 % of species occurring within 1200 m^2 of rainforest at each of five sites. In each case, the addition of pectinase during incubation did not result in any additional positive results. The test with added enzyme therefore effectively served as a replicate test for each sample. A further two species were found to be cyanogenic but were not included in the analysis—the non-woody *Alocasia brisbanensis*, and *Helicia nortoniana* which occurred outside the plots (Table 1). The number of cyanogenic species at each site ranged from four to 10. The cyanogenic species ranged in life form from climbing monocotyledons such as the supplejack, *Flagellaria indica*, to 30 m canopy trees such as the northern silky oak, *Cardwellia sublimis*. The proportion of cyanogenic species ranged from 4·7 % in upland rainforest at Mt Nomico, to 6·5 % in lowland rainforest near Cape Tribulation. Overall, cyanogenic species accounted for 7·3 % of total basal area (range 1·2–13·4 %). The highest proportion was in highland rainforest on basalt soil at Longlands Gap, while forest on rhyolite in adjacent forest had the lowest proportion. In lowland rainforest, the contribution of cyanogenic species to biomass was also high, at 11·6 %, compared with 3·3 and 7·1 % at Mt Nomico and Lamins Hill sites, respectively.

The cyanogenic species and concentrations of cyanogenic glycosides in leaves and other plant parts are summarized in Table 1. The foliar concentrations of cyanogenic glycosides among species ranged from around 8 μg CN g^{-1} d. wt—the concentration below which individuals were considered acyanogenic based on the criteria of Adsersen *et al*. (1988) and the limits of FA paper detection—to very high concentrations in excess of several mg CN g^{-1} d. wt (Table 1). For example, fully expanded

TABLE 1. *Summary of the concentration of cyanogenic glycosides in leaves and other plant tissues from cyanogenic species found in six plots in upland/highland (U) and lowland (L) tropical rainforest at five sites: high nutrient basalt sites at Lamins Hill (B1) and Longlands Gap (B2), and low nutrient sites on granite at Mt Nomico (G), on rhyolite at Longlands Gap (R) and on metamorphic substrate near Cape Tribulation (M)*

Form	Species	Family	Forest	Site	Concentration of cyanogenic glycosides in different plant parts (mg CN g^{-1} d. wt)			
					Leaf	Stem	Floral parts	Fruit/seed
H	*Alocasia brisbanensis* (F.M.Bailey) Domin*	Araceae	U	B1	–	–	–	–
T	*Beilschmiedia collina* B.Hyland	Lauraceae	U	B1, B2, G, R	Old: 28·4–1263 (n = 36) Yg: 1039–1391	–	–	–
T	*Brombya platynema* F.Muell.	Rutaceae	L	M	156·4–1285 (n = 20) 0–10·5 (n = 27)	–	–	–
T	*Cardwellia sublimis* F.Muell.	Proteaceae	U, L	B1, B1, G, R, M	Old:11·5–69·8 (n = 21) Yg: 733·1, tips: 219·1	–	Bud: 779–851 Flwr: 130–334	Seed: approx.8
T	*Cleistanthus myrianthus* (Hassk.) Kurz	Euphorbiaceae	L	M	Old: 1·1–17·3 (n = 41) Yg: 78·4–80·4 (n = 3)	–	Flwr: 30·7	Mature: 160–377 Immature: 821
T	*Clerodendrum grayi* Munir	Verbenaceae	U	B1, B2, G	Old: 1325–4800 (n = 6)	–	Bud: 733 Flwr 440–942	–
T	*Elaeocarpus sericopetalus* F.Muell.	Elaeocarpaceae	U	G, R	1100–5056 (n = 10)	Sdlg: 1739–2679 Tree: 135	–	1028
V	*Embelia grayi* S.T.Reynolds	Myrsinaceae	U	B1, B2	10–81 (n = 3)	–	–	–
V	*Flagellaria indica* L.	Flagellariaceae	U, L	B1, G, M	11–177·3 (n = 6)	–	–	–
T	*Helicia australasica* F.Muell.	Proteaceae	L	M	42·2–155·2 (n = 8)†	–	–	–
T	*Helicia blakei* Foreman	Proteaceae	U	B1	Mean: 17·9 (n = 2)	–	–	–
T	*Helicia nortoniana* (F.M.Bailey) F.M.Bailey*	Proteaceae	L	M	–	–	–	–
V	*Passiflora* sp. (Kuranda BH12896)	Passifloraceae	L	M	313–922 (n = 4)	–	–	–
T	*Mischocarpus exangulatus* (F.Muell.) Radlk.	Sapindaceae	U	B1	Old: 133; yg: 222 (n = 1)	–	–	–
T	*Mischocarpus grandissimus* (F.Muell.) Radlk.	Sapindaceae	U, L	G, M	49–680 (n = 2) 761–2006 (n = 4)‡	–	–	–
T	*Opisthiolepis heterophylla* L.S.Sm.	Proteaceae	U	B1, B2	Old: 10–208 (n = 7) Yg: 2000	–	–	–
V	*Parsonsia latifolia* (Benth.) S.T.Blake	Apocynaceae	U	B1, G, R	765–4835 (n = 3)	–	–	–
T	*Polyscias australiana* (F.Muell.) Philipson	Araliaceae	U, L	B1, B2, G, R, M	Old: <6·8 (n = 30); 10–28·5 (n = 16) Yg: 10·8–29·6; tips: 259	–	–	–
T	*Prunus turneriana* (F.M.Bailey) Kalkman	Rosaceae	U, L	B1, M	old: 2472–4888 (n = 4) Yg: 3128–6464; Tip: 6000–8498	560–1100 (n = 2) Root: approx. 2000	–	Mature seed: 400 Yg fruit/seed: 8950
T	*Ryparosa javanica* (Blume) Kurz ex Koord. & Valeton**	Achariaceae	L	M	1749 (n = 2) Yg lf: 2560 (n = 5)	–	–	Mature seed: 5430 Yg seed: 7760 (n = 5)

Means and ranges of cyanogenic glycosides concentration are given for fully expanded (old) leaves where not specified, and for some young (yg) leaves, for n individuals. Life form: herb (H), tree (T), vine (V). Cyanogenic glycoside concentrations were measured as evolved cyanide, following hydrolysis of freeze-dried tissue, without the addition of non-specific β-glycosidase (e.g. emulsin/pectinase).

* *Alocasia brisbanensis* (a herb), and *Helicia nortoniana* which occurred outside the plots, were not included in the analysis, nor sampled for quantitative analysis.

** Concentrations of cyanogenic glycosides in seed, flower and young leaves of *Ryparosa javanica* determined by B. L. Webber (unpubl data, 2004; Webber and Woodrow, 2004).

† Only one individual of *Helicia australasica* occurred within the plots; seven additional saplings/trees were opportunistically tested external to the plots; all were cyanogenic.

‡ Only one individual of *Mischocarpus grandissimus* occurred inside plots at Mt Nomico; additional individuals were sampled outside plots, including four in lowland rainforest, all were cyanogenic.

leaves of numerous individuals of *Polyscias australiana* tested negative for cyanide, and contained <8 μg CN g^{-1} d. wt, while others tested positive and were in the range of 10–28 μg CN g^{-1} d. wt. Even in the weakly cyanogenic samples, only in very few cases did the coloration of the test paper change from 12 to 24 h in a qualitative sense. Individuals of numerous species had high concentrations of cyanogenic glycosides in excess of 1 mg CN g^{-1} d. wt (e.g. *Mischocarpus grandissimus*, *Brombya platynema* and *Beilschmiedia collina*), and several species contained extremely high concentrations of cyanogenic glycosides in mature tree leaves. Notably, fully expanded leaves from the tree species *Elaeocarpus sericopetalus*, *Clerodendrum grayi* and *Prunus turneriana* had concentrations of cyanogenic glycosides up to 5·2, 4·9 and 4·8 mg CN g^{-1} d. wt, respectively (Table 1).

Qualitative and quantitative variation in cyanogenesis

Intra-population variation in cyanogenic glycosides. For the majority of species initially identified as being cyanogenic, all individuals tested were cyanogenic; however, the concentrations of cyanogenic glycosides varied markedly between conspecific individuals (Table 1). For example, all saplings and trees of *B. collina* at each site tested positive for cyanogenesis, but the concentration of cyanogenic glycosides in fully expanded leaves from saplings (n = 19) ranged from 23·2 to 1263·4 μg CN g^{-1} d. wt at Mt Nomico alone, where *B. collina* was most abundant. In contrast to this quantitative phenotypic variation in cyanogenesis, conspecific individuals of a small number of species produced both positive and negative FA paper test results. This apparent qualitative polymorphism was most notable in *B. platynema*, a subcanopy tree species restricted to the lowland rainforest. Within the population of *B. platynema*, approx. 50 % of individuals tested produced negative FA test paper results for both young and old leaves, and had cyanogenic glycoside concentrations in the range 0·6–6·8 μg CN g^{-1} d. wt (Table 1.). The addition of buffered pectinase during testing did not alter the qualitative FA paper test result for any individual. Among cyanogenic *B. platynema*, the concentrations of cyanogenic glycosides varied over orders of magnitude from 10·5 to 1285·9 μg CN g^{-1} d. wt (Table 1).

Negative results with FA papers were obtained for two other species, *Cleistanthus myrianthus* and *Polyscias australiana.* Qualitative and quantitative analysis of old leaves from individuals of these species indicated a high frequency of acyanogenic individuals; however, unlike *B. platynema*, the phenotypic expression of cyanogenesis varied qualitatively with leaf age such that young leaves and leaf tips from these same individuals were consistently cyanogenic, as were reproductive tissues from *C. myrianthus* (Table 1).

Even among less common species with small sample sizes, the concentrations of cyanogenic glycosides varied markedly between individuals. For example, in *Mischocarpus grandissimus*, the concentration among six individuals from two sites ranged from 49 to 680 μg CN g^{-1} d. wt at Mt Nomico and from 637 to 2006 μg CN g^{-1} d. wt in lowland rainforest, and among three individuals of the woody vine *Parsonsia latifolia*, concentrations ranged from 765 to 4835 μg CN g^{-1} d. wt. There was no detectable affect of soil type on qualitative determination of cyanogenesis for individuals of the same species; where cyanogenic species were found on different substrates, all individuals tested were cyanogenic.

Intra-plant variation in cyanogenic glycoside concentration. In addition to cyanogenic polymorphism, both qualitative and quantitative, within populations of cyanogenic species, the concentration of cyanogenic glycosides varied with leaf age and plant part. In all cases where tested, young leaves or leaf tips had higher concentrations of cyanogenic glycosides than older leaves (Table 1). In some cases, the concentrations in young and old leaves differed by over an order of magnitude (e.g. *C. sublimis* and *Opisthiolepis heterophylla*; Table 1). In terms of determining the cyanogenic phenotype of an individual, this difference between leaves of different ages was most notable for *C. myrianthus* and *P. australiana*. Based on FA paper tests of mature fully expanded leaves of these species, there were frequent acyanogenic individuals; however, young leaves and leaf tips sampled from the same individuals of both species routinely tested positive for cyanogenesis. Furthermore, among mature trees of *C. myrianthus*, which had low levels of cyanogenic glycosides in old leaves (6–8 μg CN g^{-1} d. wt, i.e. considered acyanogenic), the fruit, in particular, had higher concentrations of cyanogenic glycosides (>800 μg CN g^{-1} d. wt; Table 1). Overall, few tests were made of seeds or other reproductive tissues as part of the survey; however, where reproductive tissues were tested from species with cyanogenic leaves, they were typically cyanogenic and contained higher concentrations of cyanogenic glycosides, although the concentration varied with the maturity of the fruit/seed. For example, the immature seed and fruit (combined) from *Prunus turneriana* had >8 mg CN g^{-1} d. wt compared with mature seed alone (<1 mg CN g^{-1} d. wt), while in *R. javanica* cyanogenic glycoside concentrations in flesh and seed of immature fruit decreased with maturity (Table 1; Webber and Woodrow, 2004). One exception was the papery wind-dispersed seeds of *C. sublimis* which yielded negligible cyanide (Table 1).

DISCUSSION

Cyanogenic species

Despite a substantial body of early work screening Australian flora, including some tropical flora, for cyanogenesis (e.g. Petrie, 1912; Smith and White, 1918; Finnemore and Cox, 1928; Hurst, 1942; Webb, 1948, 1949), few of the species tested in this study had previously been tested. Of the 18 species from 13 families found to be cyanogenic in this study, only one, *F. indica*, has previously been reported as cyanogenic (Petrie, 1912). Thirteen of the cyanogenic species are endemic to Queensland or Australia; several are restricted to small areas within north east Queensland. For example, *Clerodendrum grayi* is found only in a small area on the Atherton Tableland (Miller *et al.*, 2006*a*), while

R. javanica occurs in a limited area within lowland rainforest north of the Daintree River. Cyanogenesis is reported for the first time in the genera *Beilschmiedia*, *Cardwellia*, *Cleistanthus*, *Elaeocarpus*, *Embelia*, *Mischocarpus*, *Opisthiolepis*, *Parsonsia* and *Polyscias*. The number of new reports at the generic level may in part reflect the high level of endemism among the Australian tropical rainforest flora. In addition, several species are from families in which cyanogenesis has been rarely reported, if at all. For example, cyanogenesis is rare in Elaeocarpaceae, Lauraceae, Apocynaceae, Myrsinaceae and Araliaceae families. Following are descriptions of each cyanogenic species (listed alphabetically by family) discussed in relation to previous reports of cyanogenesis within the relevant taxonomic groups.

Ryparosa javanica (Blume) Kurz ex Koord. & Valeton (Achariaceae)

Ryparosa javanica is currently the subject of taxonomic revision (Webber, 2005). The Queensland *Ryparosa* sp. currently known as *R. javanica* is endemic to lowland rainforest north of the Daintree River to Cape Tribulation, north east Queensland. This species was found to be cyanogenic early in this survey, and has subsequently been the focus of extensive population-level studies of cyanogenesis (Webber, 2005). Reports of cyanogenesis in this genus are common; for example, *R. javanica* (*sensu stricto*) and *R. caesia* are cyanogenic (Rosenthaler, 1919). Cyanogenesis has been reported among other genera in Achariaceae, e.g. *Hydnocarpus*, *Calancoba*, *Ceratiosicyos*, *Gynocardia*, *Erythrospermum*, *Pangium* and *Kiggelaria* (Rosenthaler, 1919; Tjon Sie Fat, 1979*a*; Jensen and Nielsen, 1986). Many of these genera were previously in the Flacourtiaceae until recent revisions saw most cyanogenic genera assigned to the Achariaceae (Chase *et al*., 2002), including the tribe Pangieae of which *Ryparosa* is a member. Cyanogenesis was considered a useful taxonomic marker in Flacourtiaceae (Spencer and Seigler, 1985), this utility being apparent in the revision of the family (Chase *et al*., 2002). All individuals in sizeable populations of *R. javanica* were cyanogenic, and the cyanogenic glycoside in *R. javanica* has been identified as gynocardin (Webber, 2005), a cyclopentenoid cyanogenic glycoside typical of Achariaceae (Jaroszewski and Olafsdottir, 1987). Cyanogenic glycosides derived from valine/isoleucine have also been reported in species formerly in the Flacourtiaceae (Lechtenberg and Nahrstedt, 1999).

Parsonsia latifolia (Benth.) S.T.Blake (Apocynaceae)

This is the first report of cyanogenesis in the genus *Parsonsia*, a genus of woody or semi-woody climbers (130 species) distributed from Southeast Asia to Australia, New Caledonia and New Zealand. Members of the Apocynaceae family (220 genera, 2000 species) commonly have clear or milky latex, and frequently contain alkaloids (Mabberley, 1990; Collins *et al*., 1990). *Parsonia latifolia* (diameter up to 9 cm) has milky white latex, and is endemic to Australia (Forster and Williams, 1996). It is found in lowland and highland rainforest in noth east Queensland, parts of New South Wales and the Northern Territory (Hyland *et al*., 2003). Reports of cyanogenesis in Apocynaceae and the order Gentianales are few; Gibbs (1974), who reported negative results for *Parsonsia eucalyptifolia* and *P. lanceolata*, found only *Alstonia scholaris* (L.) R.Br. to be cyanogenic, and noted positive reports for four other species. Tests for cyanogenesis in the Apocynaceae are, however, apparently limited, with negative reports for only approx. 20 species (Gibbs, 1974; Adsersen *et al*., 1988; Thomsen and Brimer, 1997). In this study, leaf samples of all ages from multiple *A. scholaris* trees and seedlings gave negative FA paper results; quantitative assaying confirmed the absence of cyanogenesis. No cyanogenic constituents in the family have been characterized.

Polyscias australiana (F.Muell.) Philipson (Araliaceae)

This is the first report of cyanogenesis in the genus *Polyscias*, a genus of approx. 100 species distributed throughout Africa, Asia, Malesia, Australia and the Pacific Islands. In addition, cyanogenesis is very rare in the order Umbellales; Gibbs (1974) reported only negative results or some doubtful positive results in a few members of Araliaceae (*Nothopanax* sp. and *Schefflera* sp.) and the Umbelliferae. Subsequently, only *Aralia spinosa* L. (above-ground parts) has been reported as cyanogenic (Seigler, 1976b). *Polyscias australiana* is often considered a regrowth species in disturbed rainforest, and commonly occurs at rainforest margins. Concentrations of cyanogenic glycosides in this species were variable, and in mature leaves were commonly less than the threshold value used for classifying individuals as cyanogenic in this study (<8 μg CN g^{-1} d wt); however, the species was considered cyanogenic on the basis of repeatable positive results with FA papers for multiple individuals, in particular when analysing young foliage. Interestingly, in reporting cyanogenesis in *A. spinosa*, Seigler (1976*b*) noted substantial seasonal variation, in that the individual was cyanogenic at only one of three testing times throughout the year. Analysis of the distribution of cyanogenic glycosides in fruit, flowers and seasonal variation in foliar concentrations in *P. australiana* would better characterize cyanogenesis in this species.

Elaeocarpus sericopetalus F.Muell. (Elaeocarpaceae)

Elaeocarpus sericopetalus ('Northern Quandong') is a small to medium sized tree endemic to tropical rainforest within the Cook and Kennedy Districts of north eastern Queensland. This is the first report of cyanogenesis in the genus *Elaeocarpus*. *Elaeocarpus sericopetalus* was the only cyanogenic species identified among eight *Elaeocarpus* spp. and 11 species from the Elaeocarpaceae family tested in this study (Appendix). The extremely high foliar concentrations of cyanogenic glycosides (up to 5·2 mg CN g^{-1} d. wt in mature field-grown leaves) in *E. sericopetalus* rank it among the most cyanogenic tree species ever reported. Cyanogenesis is rare within the family Elaeocarpaceae and the order Malvales (Gibbs, 1974; Hegnauer, 1990; Lechtenberg and Nahrstedt, 1999), whereas alkaloids (e.g. indolizidine alkaloids) are

considered common (Gibbs, 1974; Hegnauer, 1990; Mabberley, 1990). In the Elaeocarpaceae family, cyanogenesis has previously been reported in only two species: the leaves of *Vallea stipularis* '*pyrifolia*' F.Ballard (Gibbs 1974), and the leaves [Greshoff (1898) cited in Hegnauer (1973)] and the bark (Pammel, 1911; Rosenthaler, 1919) of *Sloanea sigun* (Blume) K.Schum (syn. *Echinocarpus sigun*), were found to be cyanogenic. Sambunigrin was isolated from the leaves of *S. sigun* [R. Hegnauer and L. H. Fikenscher, unpubl. data (1983) cited in Hegnauer (1990)], the only previous report of a cyanogenic constituent in Elaeocarpaceae and Malvales. Characterization of the principal foliar cyanogenic glycoside—an apparently unusual phenylalanine-derived glycoside with an organic acid residue—is ongoing (Miller, 2004).

Cleistanthus myrianthus (Hassk.) Kurz (Euphorbiaceae)

This appears to be the first report of cyanogenesis in the genus *Cleistanthus*, which consists of 100–140 species. *Cleistanthus myrianthus* is a subcanopy rainforest tree (to 7 m), found in the lowland and foothills from the Daintree River to Rossville, north east Queensland (Cooper and Cooper, 1994). In Australia, it is classified as rare on the basis of this limited distribution, but it is also found in Southeast Asia and Malesia (Hyland *et al*., 2003). Cyanogenesis is especially common in Euphorbiaceae (300 genera, 7500 species), and is found in many genera including *Bridelia*, *Euphorbia* and *Phyllanthus*, as well as the economically important species *Hevea brasiliensis* (rubber tree) and *Manihot esculenta* (cassava) (e.g. Rosenthaler, 1919; Tjon Sie Fat, 1979*a*; Seigler *et al*., 1979; Adsersen *et al*., 1988).

The chemotaxonomic utility of cyanogenesis, as well as other secondary metabolites (e.g. alkaloids and terpenes), has been demonstrated in Euphorbiaceae (Seigler, 1994). Cyanogenic glycosides are useful at the infra-familial level in the Euphorbiaceae (van Valen, 1978; Seigler, 1994); the species in the subfamily Phyllanthoideae typically contain the tyrosine-derived cyanogenic glycosides dhurrin, taxiphyllin or triglochinin, while species in the subfamily Crotonoideae (*sensu* Pax and Hoffman, 1931; see van Valen, 1978), including *Hevea* and *Manihot*, produce cyanogenic glycosides derived from valine and isoleucine (e.g. linamarin and lotaustralin) (van Valen, 1978, Nahrstedt, 1987; Seigler, 1994). Given this pattern, one may predict *Cleistanthus*—assigned to the Phyllanthoideae—to contain cyanogens derived from tyrosine.

Flagellaria indica L. (Flagellariaceae)

Flagellaria indica ('the supplejack'), a leaf tendril climber with cane-like stems, is known to be cyanogenic (Petrie, 1912; Webb, 1948; Gibbs, 1974; Morley and Toelken, 1983). Young shoots were suspected of poisoning stock in Australia (Everist, 1981), and it has also been reported to have medicinal properties (e.g. tumour inhibition; Collins *et al*., 1990). In other countries, it has been used as a hair wash, and as a contraceptive (see Hyland *et al*., 2003), but was not apparently used medicinally by aboriginal Australians (Morley and Toelken, 1983). Interestingly, monocotyledons are typically characterized by cyanogenic glycosides biosynthetically derived from tyrosine (Lechtenberg and Nahrstedt, 1999). Consistent with this, the tyrosine-derived cyanogenic glycoside triglochinin was isolated from the stem (and rhizome) of *F. indica* (L. H. Fikenscher unpubl. data, cited in Hegnauer, 1966), although meta-hydroxylated valine or isoleucine, and leucine-derived glycosides have also been found in monocotyledons (Nahrstedt, 1987; Lechtenberg and Nahrstedt, 1999).

Clerodendrum grayi Munir (Lamiaceae)

Clerodendrum grayi is a rare subcanopy tree endemic to the northern part of Queensland, Australia (Munir, 1989). Recent revisions of the division between Lamiaceae and Verbenaceae families (Cantino, 1992; Wagstaff *et al*., 1997, 1998) transferred the genus *Clerodendrum*, and others historically in the Verbenaceae family, to the Lamiaceae family. Cyanogenesis in Lamiaceae, and also Verbenaceae, has rarely been reported. Even within the order Lamiales, cyanogenesis is considered rare (Gibbs, 1974). In the Lamiaceae, known for its culinary and medicinal herbs [e.g. *Lavandula* (lavender); *Mentha* (mint)], typical constituents are monoterpenoids, diterpenes or triterpenes, as well as flavonoids and iridoid glycosides (Gibbs, 1974; Hegnauer, 1989; Taskova *et al*., 1997). In a survey of the flora of the Galapagos Islands, *Clerodendrum molle* var. *molle* was found to be cyanogenic (Adsersen *et al*., 1988; see also Gibbs, 1974, Tjon sie Fat, 1979*a*). In addition, several species of *Clerodendrum* are known to be toxic (Hurst, 1942; Webb, 1948; CFSAN, 2003); however, the poison is not detailed.

In this study, the extremely high foliar concentrations of cyanogenic compounds—up to $4{\cdot}8\ \mathrm{mg\ CN\ g^{-1}\ d.wt}$ in mature field-grown tree leaves—are among the highest reported for tree leaves (Table 1). Two cyanogenic glycosides were purified from the leaf tissue of *C. grayi* (Miller *et al*., 2006*a*). Prunasin and its primerveroside, the rare diglycoside lucumin (Eyjólfsson, 1971), were found in the ratio 1 : 1·58 (mol:mol) (Miller *et al*., 2006*a*), the first reported co-occurrence of these glycosides, and the first confirmed report of lucumin in vegetative tissue (see Thomsen and Brimer, 1997). Given the relatively rarity of reports of cyanogenic glycosides from the Lamiaceae, and even within the order Lamiales, it is difficult to draw any conclusions about the biogenetic origins of glycosides within these taxonomic groups. Refer to Miller *et al*. (2006*a*) for a detailed discussion of cyanogenesis in *C. grayi* and associated taxa.

Beilschmiedia collina B.Hyland (Lauraceae)

Beilschmiedia collina ('the mountain blush walnut') is a tree species endemic to Queensland rainforest (Cooper and Cooper, 1994). Cyanogenesis is very rare in Lauraceae (Gibbs, 1974; Hegnauer, 1989), having only been reported from *Cinnamomum camphora* and *Litsea glutinosa* (Gibbs, 1974), with one other species (*Nectranda megapotamica*) reported to have cyanogenic glycosides but apparently lacks the catabolic enzymes, requiring further investigation

(Francisco and Pinotti, 2000). The Lauraceae is better known for producing a range of alkaloids (e.g. Gibbs, 1974), and as a dominant family in the rainforest flora of Australia has been much studied for its toxic and potentially medicinal alkaloids (Webb, 1949, 1952; Collins *et al*., 1990). Of 39 species tested in the Lauraceae family in this survey, only *B. collina* was cyanogenic (Appendix). Given the apparent rarity of cyanogenesis in the family, and even the order Laurales, it is difficult to speculate as to the biosynthetic precursor of the cyanogenic constituent in *B. collina*. To the authors' knowledge, only the tyrosine-derived cyanogenic glycoside taxiphyllin has been reported in the Calycanthaceae family within the Laurales (Lechtenberg and Nahrstedt, 1999); tyrosine-derived glycosides are also found in Ranunculaceae in the order Ranunculales, which is in the same subclass Magnoliidae (*sensu* Cronquist, 1981) as Laurales.

Embelia grayi S.T. Reynolds (Myrsinaceae)

This is the first report of cyanogenesis in the genus *Embelia*—a genus of approx. 130 species—and among the first in the family Myrsinaceae. Furthermore, Gibbs (1974) considered cyanogenesis to be unknown in the order Primulales. Subsequent to Gibbs (1974), only two reports of cyanogenesis in Myrsinaceae could be found—for *Rapanea parviflora* (Kaplan *et al*., 1983), and for *R. umbellata*, which needs confirmation as cyanogenesis was only detected after 24 h of tissue incubation (Francisco and Pinotti, 2000). Overall, there are even a few negative test records for the family. *Embelia grayi* is a vine with diameter up to 9 cm, endemic to upland and highland rainforest in north east Queensland. *Embelia caulialata*, and three *Rapanea* spp., also tested here, were not cyanogenic. The order Primulales (*sensu* Cronquist, 1981) is in the subclass Dilleniidae which also includes the orders Malvales and Violales. Within the Violales, cyanogenesis is common in the Achariaceae (including Flacourtiaceae), Passifloraceae and Turneraceae families, which tend to contain cyanogenic glycosides of the cyclopentanoid series (Lechtenberg and Nahrstedt, 1999).

Passiflora sp. (Kuranda BH12896) (Passifloraceae)

Passiflora sp. (Kuranda BH12896) was the only species in the Passifloraceae tested in this study. It is a vine found in the lowland rainforests of north east Queensland; all Australian members of the Passifloraceae are climbers or sprawling shrubs (Morley and Toelken, 1983). Cyanogenesis is common within the family Passifloraceae (600 species, two genera worldwide), and the genus *Passiflora* (e.g. Rosenthaler, 1919; Tjon Sie Fat, 1979*a*; Adsersen *et al*., 1988; Olafsdottir *et al*., 1989). Several Australian *Passiflora* spp. were reported to be cyanogenic, including *P. aurantia* (Petrie, 1912; Smith and White, 1918; Webb, 1952; Gardner and Bennetts, 1956) and the endemic *P. herbertiana* Lindl. (Petrie, 1912), and implicated in poisoning stock (Smith and White, 1918). Within Passifloraceae, cyanogenesis has also been reported in *Adenia* spp. and *Ophiocaulon* spp. (Rosenthaler, 1919; Tjon Sie Fat, 1979*a*). The specific cyanogenic constituents may be taxonomically diagnostic at the infrafamilial level (e.g. occurrence of the rare glycoside passibiflorin; Adsersen *et al*., 1993). Cyanogenic Passifloraceae typically contain cyanogenic glycosides with cyclopentenoid ring structures (Seigler *et al*., 1982; Spencer and Seigler, 1985; Nahrstedt, 1987; Lechtenberg and Nahrstedt, 1999), although phenylalanine-derived glycosides (e.g. prunasin) have been isolated from *Passiflora edulis* (Spencer and Seigler, 1983; Chassagne *et al*., 1996; Seigler *et al*., 2002), and valine/isoleucine-derived glycosides (e.g. linamarin, lotaustralin) from several *Passiflora* spp. in the subgenus Plectostemma (Spencer *et al*., 1986).

Cyanogenesis in the Proteaceae family

Five of the 20 species tested in the Proteaceae family were found to be cyanogenic: *C. sublimis* F.Muell., *O. heterophylla* L.S.Sm., *Helicia australasica* F.Muell, *H. blakei* Foreman and *H. nortoniana* (F.M.Bailey) F.M.Bailey. The latter species was opportunistically tested as it was found only outside the plots. This is the first formal report of cyanogenesis in the monospecific genera *Cardwellia* and *Opisthiolepis*, while cyanogenesis has previously been reported in the genus *Helicia* (*H. robusta*; Gibbs, 1974).

Cardwellia sublimis ('the northern silky oak') is the only species in the tribe Cardwelliinae (Hoot and Douglas, 1998). This canopy species (to 30 m), an important timber tree, is endemic to north east Queensland, being widely distributed throughout well-developed lowland to highland rainforest (Hyland *et al*., 2003). *Cardwellia sublimis* was common to all sites in this study.

Opisthiolepis heterophylla ('the blush silky oak') is endemic and confined to north east Queensland, from the Kirrama Range to Cooktown. It grows to 30 m in lowland to highland rainforest, but is most common in upland and highland rainforest on the Atherton Tableland (Hyland *et al*., 2003). The flowers of *O. heterophylla* have been found to be cyanogenic (E. E. Conn, University of California, Davis, CA, USA, pers. comm.).

The genus *Helicia* (approx. 90 species) occurs throughout Asia and the Pacific, with nine species found naturally in Australia (Foreman, 1995). *Helicia blakei* ('Blake's silky oak') is endemic to north east Queensland, occurring as an understorey tree in well-developed upland rainforest (Hyland *et al*., 2003). *Helicia australasica* is a shrub or tree (3–20 m) widespread throughout northern Australian through to Papua New Guinea. It occurs as an understorey tree in well-developed rainforest, monsoon forest and dry rainforest (Foreman, 1995; Hyland *et al*., 2003). The fruit is known to be eaten by aborigines (Foreman, 1995). *Helicia nortoniana* is also an understorey tree (to 20 m), endemic to north east Queensland, and found in well-developed lowland and highland rainforest (Cooper and Cooper, 1994; Foreman, 1995; Hyland *et al*., 2003). These data support the preliminary results of tests on dried herbarium samples where only some samples of *H. australasica* and *H. nortoniana* tested positive for cyanide (E. E. Conn, University of California, Davis, CA, USA, pers. comm.). Tests of dried herbarium samples of *H. blakei*, however, gave only negative results (E. E. Conn, University of

California, Davis, CA, USA, pers. comm.). The inconsistent findings by Conn are probably the result of using dried herbarium material.

Cyanogenesis is considered especially common in the Proteaceae (Swenson *et al*., 1989; Lechtenberg and Nahrstedt, 1999), known in a range of genera, but particularly in *Grevillea* and *Hakea* spp. In Australia, cyanogenic members of the Proteaceae have been implicated in stock poisoning (Gardner and Bennetts, 1956). Based on the reports of Gibbs (1974) and Tjon Sie Fat (1979*a*), and the study of Swenson *et al*. (1989) who found 44 of 155 proteaceous species tested to be cyanogenic, cyanogenesis is most widespread in the subfamily Grevilleoideae. For example, cyanogenesis has been reported in the genera *Stenocarpus*, *Lomatia*, *Helicia*, *Xylomelum*, *Telopea*, *Macadamia*, *Hicksbeachia*, *Lambertia*, *Grevillea* and *Xylomelum* (Petrie, 1912; Smith and White, 1918; Hurst, 1942; Gardner and Bennetts, 1956; Gibbs, 1974; Swenson *et al*., 1989; Lamont, 1993; E. E. Conn, University of California, Davis, CA, USA, pers. comm.), all of which are in the Grevilloiedeae (Hoot and Douglas, 1998). Consistent with this pattern, the cyanogenic genera reported here are all in the subfamily Grevilleoideae; *Cardwellia* in the subtribe Cardwelliinae (tribe Knightieae), *Opisthiolepis* in the subtribe Buckinghamiinae (tribe Embothrieae), and *Helicia* in the subtribe Heliciinae (tribe Heliceae). In contrast, there are only a few reports of cyanogenesis within the Proteoideae subfamily; cyanogenesis was only reported in single species of *Conospermum*, *Petrophile* and *Protea* (Gibbs, 1974; Swenson *et al*., 1989; E. E. Conn, University of California, Davis, CA, USA, pers. comm.).

The cyanogenic constituents, which have been identified in comparatively few species, appear to be biogenetically derived from tyrosine. Swenson *et al*. (1989) identified the cyanogenic glycosides in eight species; leaves and flowers of several *Hakea*, *Leucadendron*, *Grevillea* and *Macadamia* species were found to contain dhurrin and proteacin (see also Plouvier, 1964; Young and Hamilton, 1966). In this regard, the identity of the cyanogenic constituent in the monospecific genera in particular would be interesting.

Prunus turneriana (F.M.Bailey) Kalkman (Rosaceae)

Cyanogenesis is widespread within Rosaceae (Hegnauer, 1990), and has been much studied in the subfamily Prunoideae in particular, as it contains many cyanogenic cultivated species [e.g. *Prunus domestica* L. (plum); *Armeniaca vulgaris* Lam. (apricot)]. Cyanogenic Rosaceae (in particular *Prunus* spp.) are also a common source of poisoning in domestic animals (e.g. Poulton, 1983; Schuster and James, 1988). *Prunus turneriana* is one of only two *Prunus* species native to Australia and is a late successional canopy tree species in the lowland and upland rainforests of far north Queensland, Australia. The fruits of this canopy species are known to be toxic, yet are also eaten by cassowaries, fruit pigeons, Herbert river ringtail possums and musky-rat kangaroos (Cooper and Cooper, 1994). The flesh of the fruit was used raw by the Ngadjonji people—the original inhabitants of the rainforests on the Atherton Tablelands, north Queensland—for treating toothache, while the toxic kernels were processed for a starchy food (Huxley, 2003). Despite its common name 'Almond bark' and phytochemical surveys of Australian rainforest species (e.g. Webb, 1949), cyanogenesis in *P. turneriana* had not previously been reported. Cyanogenic glycosides were found to be distributed throughout all tissues and, consistent with other species in the Rosaceae, are biosynthetically derived from the amino acid phenylalanine (Møller and Seigler, 1999). Prunasin was identified as the major cyanogen in leaf, stem, root and seed tissues of *P. turneriana*, and amygdalin was restricted to the seed. What was unusual about *P. turneriana* was the presence of significant amounts of the (*R*)-prunasin epimer, (*S*)-sambunigrin, in leaf, stem and seed tissue, whereas root tissue contained only prunasin. Refer to Miller *et al*. (2004) for the detailed characterization of cyanogenesis in *P. turneriana*.

Brombya platynema F.Muell. (Rutaceae)

This is the first report of cyanogenesis in the genus *Brombya*, which is a genus of 1–2 species endemic to Australia (Hyland *et al*., 2003). *Brombya platynema* is endemic to north east Queensland where it occurs as an understorey tree in well-developed forest (from sea level to 1100 m a.s.l.) (Hyland *et al*., 2003). The family (150 genera, 1500 species) includes many strongly scented shrubs and trees, and rutaceous species are known for their terpenoids and alkaloids (Price, 1963; Gibbs, 1974; Everist, 1981). Cyanogenesis is rare in Rutaceae, and has only been reported in *Boronia bipinnate* Lindl. (leaves; Rosenthaler, 1919), *Zieria* spp. (Hurst, 1942; Gibbs, 1974; Fikenscher and Hegnauer, 1977), *Zanthoxylum fagara* (Adsersen *et al*., 1988) and *Loureira cochinchinensis* Meissa (Gibbs, 1974). Even within the order Rutales, cyanogenesis is rare, with only a few additional definitive reports of cyanogenesis in the Tremandraceae family (Gibbs, 1974). The phenylalanine-derived cyanogenic glycosides prunasin/sambunigrin and zierin have been isolated from leaves of two *Zieria* spp. (Finnemore and Cooper, 1936; Fikenscher and Hegnauer, 1977). The rare meta-hydroxylated cyanogenic glycoside holocalin was recently identified as the principal cyanogen in leaves of *B. platynema*; traces of prunasin and amygdalin were also detected (Miller *et al*., 2006*b*). These data suggest the possibility that species in this family have cyanogenic glycosides biosynthetically derived from the amino acid phenylalanine.

Mischocarpus grandissimus (F.Muell.) Radlk. and *Mischocarpus exangulatus* (F.Muell.) Radlk. (Sapindaceae)

Two of the four species of *Mischocarpus* tested in this study were found to be cyanogenic—*M. grandissimus* and *M. exangulatus*—representing the first reports of cyanogenesis for the genus. *Mischocarpus* is a genus of 15 species found in Asia, Malesia and Australia; nine species occur naturally in Australia (Hyland *et al*., 2003). Both species are endemic to Queensland; *M. grandissimus* is restricted to north east Queensland, while *M. exangulatus* is also found on the Cape York Peninsula, Queensland. *Mischocarpus*

grandissimus occurs as an understorey tree in well-developed lowland and upland rainforest (sea level to 750 m a.s.l.; Hyland *et al*., 2003). Similarly, *M. exangulatus* ('the red bell mischocarp') is an understorey tree to 15 m found in well-developed lowland and highland rainforest (sea level to 1100 m a.s.l.; Cooper and Cooper, 1994; Hyland *et al*., 2003). These were the only cyanogenic species identified among the 29 species in the Sapindaceae family tested in this study (Appendix). Cyanogenesis is known in the Sapindaceae family; however, the family is best known for cyanolipids in the seed oils of numerous species (e.g. *Alectryon* spp., *Allophylus* spp., *Cardiospermum* spp., *Sapindus* spp., *Paullinia* spp. and *Ungnadia speciosa*) (Mikolajczak *et al*., 1970; Seigler *et al*., 1971; Gowrikumar *et al*., 1976; Seigler and Kawahara, 1976). There are only a few reports of cyanogenesis in Australian indigenous members of Sapindaceae—for *Dodonaea* spp. (Hurst, 1942; Webb, 1949) and *Alectryon* spp. (Smith and White 1918; Finnemore and Cooper, 1938)—and, with the exception of *Heterodendrum oleifolium* Desf. [syn. *Alectryon oleifolius* (Desf.) S.Reyn], the cyanogenic constituents in these species have not been characterized. In addition to cyanolipids in the seeds, leucine-derived cyanogenic glycosides have been characterized from vegetative parts of sapindaceous species (Seigler *et al*., 1974; Hübel and Nahrstedt, 1975, 1979; Nahrstedt, and Hübel, 1978).

Further findings

Alocasia brisbanensis (Araceae) was also found to be cyanogenic, consistent with reports of cyanogenesis in numerous congeneric species (Rosenthaler, 1919; Tjon Sie Fat, 1979*a*). However, as a herb, it was not included in the analysis. The tyrosine-derived cyanogenic glycoside triglochinin has been isolated from the closely related *A. macrorrhiza* (Nahrstedt, 1975).

There were several findings which contradicted previous reports for species. In addition to negative results for *A. scholaris* noted above, *Eupomatia laurina* (Eupomatiaceae) was reported to be 'doubtfully cyanogenic' and *Cananga odorata* (Annonaceae) cyanogenic by Gibbs (1974), but neither species was found to be cyanogenic in this study (based on repeated tests of four and two individuals, respectively). Similarly, reports of cyanogenesis in fruit and leaves of the Australian endemic Davidson's plum (*Davidsonia pruriens*) (Petrie, 1912; Rosenthaler, 1929) were not corroborated, both mature leaves and fruit testing negative in this study. Gibbs (1974) also only found negative results for leaves of *D. pruriens*. In addition, negative test results for cyanogenesis in this study corroborate previous negative reports for *Neolitsea dealbata* (syn. *Litsea dealbata*), *Cayratia acris*, *Morinda jasminoides* and *Sarcopetalum harveyanum* (Gibbs, 1974; Appendix). A screening of Australian Proteaceae family, conducted primarily using dry herbarium material, was carried out by E. E. Conn (University of California, Davis, CA, USA, pers. comm.) and included several species tested in this study. As noted above, Conn had some inconsistent, and possibly therefore inconclusive, results for a number of species, which were confirmed by fresh sampling in this study. One of eight samples of *Musgravea heterophylla* gave a positive reaction after 12 h in Conn's survey, a species which was not found to be cyanogenic here. Further testing of *M. heterophylla* is warranted. As far as could be discerned, the majority of species tested in this study had not previously been tested, despite numerous screenings of Australian and Queensland plants, most notably by Webb (1948, 1949).

General findings: frequency of cyanogenesis

Of 401 species from 87 families tested in the survey, 18 (4·5 %) species from 13 families were cyanogenic. The proportion of cyanogenic species at the sites ranged from 4·7 to 6·5 %, values similar to the frequency of cyanogenic species found in a substantial survey of woody species in Costa Rican rainforest (Thomsen and Brimer, 1997)—the only previous study to report the frequency of cyanogenesis standardized with respect to plant size (dbh >10 cm) and forest area (7 × 1 ha plots). Overall, Thomsen and Brimer (1997) found that 4·0 % (range 2·1–5·7 % for plots) of 401 species from 68 families were cyanogenic, and that cyanogenic stems (dbh $\geqslant$ 5 cm) accounted for 3 % of total basal area (range 1·6–5·1 %). Here, the overall proportion of total basal area in cyanogenic stems was 7·3 % and ranged from 1·2 to 13·4 %. The highest proportions were in highland rainforest on basalt soil (13·4 %) and in lowland rainforest (11·6 %). Highland rainforest on rhyolite had the lowest proportion.

Overall, at a community level, there are few studies with which to compare frequencies of cyanogenesis reported here for tropical rainforest in north east Queensland. In the first instance, there have been few studies in tropical systems, but also, the screening methodology varies depending on the research question being addressed, be it taxonomic (e.g. examining chemical differences in relation to proposed phylogenetic relationships) or ecological (e.g. the role of secondary compounds in plant–animal interactions). For example, while the survey of Thomsen and Brimer (1997) was standardized with respect to plant size and forest area, the few surveys in other tropical systems have focused on plant–animal interactions, and have not screened in a standardized fashion. Only 2·3 % (one species) was found to be cyanogenic in the screening of >90 % of the flora ($n = 43$ species) in a species-poor seasonal cloud forest in India (Mali and Borges, 2003). In contrast, in a survey examining the frequency of cyanogenesis in relation to environmental factors and insect density along a transect from the shoreline to an inland lagoon in a neotropical woodland ('restinga'), Kaplan *et al*. (1983) found 25 species (23 %) of 108 species screened to be cyanogenic. They also reported variable test results for a further 49 species (for $n =$ 2–16 individuals), elevating the proportion of cyanogenic species to 68 %, a value which requires further examination before interpretation, as the sampling strategy (e.g. plant size, random sampling strategy, life form and transect area) was unclear, and some uncertainty with regard to picrate paper test results was expressed by the authors (Kaplan *et al*., 1983).

Adsersen *et al*. (1988) compared frequencies of cyanogenesis within the endemic and non-endemic flora of the Galapagos Islands, two floras subject to different suites of

herbivores over a period of time. They screened fresh and herbarium specimens of a significant proportion (65 %) of the flora from the Archipelago, and reported 8·1 % of endemic species, and 5·3 % of native species—those which also occur on the South American mainland—to be cyanogenic. Interestingly, they also reported a further 22 % of native species and 30 % of endemic species to release cyanide in the presence of a crude mix of β-glycosidases (including 5 % β-glucuronidase from snails), suggesting that a large number of species contain cyanogenic glycosides but lack the catabolic β-glycoside enzyme. This contrasts with the findings of several other studies where the addition of non-specific β-glycosidases or pectinase during qualitative testing did not alter the frequency of positive results (e.g. Petrie, 1912; Thomsen and Brimer, 1997; Buhrmester *et al*., 2000; Lewis and Zona, 2000; but see Conn *et al*., 1985). Similarly, in this study, all samples were spontaneously cyanogenic without the addition of pectinase from *Rhizopus* spp., indicating that non-cyanogenic individuals probably lacked both the cyanogenic glycoside and β-glycosidase, or possibly that pectinase was not able to catalyse the cyanogenesis in these species. It is perhaps noteworthy that the greater frequency of cyanogenesis reported by Conn *et al*. (1985) in response to the addition of β-glycosidase (emulsin) was in a survey solely of the genus *Acacia*, indicating that such a response may vary among taxa.

It is important to note that the frequencies reported in all of these surveys were apparently based on the testing of single specimens of the vast majority of species (Adsersen *et al*., 1988; Thomsen and Brimer, 1997; Mali and Borges, 2003). Similarly, while the present study aimed to test at least three individuals of each species in duplicate (i.e. with and without added enzyme), only one individual of many species was encountered (Appendix). Furthermore most species here were also tested in both wet and dry seasons. A range of studies report variable positive and negative test results among sample sizes as small as $n = 2$ (e.g. Kaplan *et al*., 1983; Thomsen and Brimer, 1997). Given such polymorphism for cyanogenesis (see also Aikman *et al*., 1996), the reported frequencies in these surveys may underestimate overall the actual proportion of cyanogenic species in plant communities. The reported frequency of cyanogenesis may also vary with the plant part tested. In the Costa Rican study, Thomsen and Brimer (1997) reported a greater frequency of cyanogenesis among reproductive plant parts than leaves, as did Buhrmester *et al*. (2000) in populations of *Sambucus canadensis* (elderberry) in Illinois. Consistent with that trend, individuals of species with weakly cyanogenic leaves, including some which produced negative FA paper results, had higher concentrations of glycosides in flowers or fruits; however, overall, only a small number of reproductive tissues were tested, so limited comparison can be drawn (Table 1).

The frequency of cyanogenesis varies between taxonomic groups and with life form. Cyanogenesis is considered especially common in some plant families (e.g. Rosaceae, Euphorbiaceae, Passifloraceae and Proteaceae; Lechtenberg and Nahrstedt, 1999), and rare or absent in others (e.g. Lauraceae and Araliaceae; Gibbs, 1974; Hegnauer, 1989), a trend which may in part reflect differential intensity of testing among taxonomic groups. In this study, the frequency of cyanogenesis among the dominant plant families varied. In the Proteaceae family, five of 20 (25 %) species were cyanogenic, while two of 29 (6·9 %) species in the Sapindaceae, and one of 39 (2·5 %) species in the Lauraceae were cyanogenic (Table 1). In a screening of Australian *Acacia*, 6·9 % of 360 species were cyanogenic (Conn *et al*., 1985). Cyanogenesis appears to be rare among palms; only two species (1·2 %) of 155 species of palms (108 genera) were found to be cyanogenic (Lewis and Zona, 2000). No cyanogenic palm species were identified in this study.

Concentrations of cyanogenic glycosides

Several of the 18 cyanogenic species detected in this study contained concentrations of cyanogenic glycosides among the highest reported for leaves of woody species. Most notably, tree species *E. sericopetalus*, *C. grayi* and *P. turneriana* had foliar concentrations of cyanogenic glycosides up to 5·2, 4·9 and 4·8 mg CN g^{-1} d. wt, respectively (Table 1). Similarly, Webber (1999) recorded concentrations up to 5 mg CN g^{-1} d. wt in the tree species *R. javanica*; individuals of that species occurring within the survey area of this study had a lower mean concentration of 1·8 mg CN g^{-1} d. wt (Table 1). These high concentrations are substantially greater than the majority of values reported for foliage from a range of tropical and temperate taxa. For example, concentrations up to 1·1 mg HCN g^{-1} d. wt were reported in the tropical shrub *Turnera ulmifolia* (Shore and Obrist, 1992; Schappert and Shore, 1999), while the highest concentrations in naturally occurring populations of Australian *Eucalyptus* spp. were 2·59 mg CN g^{-1} d. wt and 3·16 mg CN g^{-1} d. wt for *E. cladocalyx* and *E. yarraensis*, respectively (Gleadow and Woodrow, 2000*a*; Goodger and Woodrow, 2002). Foliar concentrations of between 1·66 and 3·78 mg HCN g^{-1} d. wt have been recorded in cultivated *Prunus* spp. (Santamour, 1998). To our knowledge, possibly the highest foliar cyanogenic glycoside concentration among naturally occurring woody species was reported in the tropical proteaceous species *Panopsis costaricensis* by Thomsen and Brimer (1997), who measured 2150 mg HCN kg^{-1} f. wt (approximately equivalent to 7·2 mg HCN g^{-1} d. wt using a conversion based on the mean foliar water content of several species in this study, which was 70 %). The age of the leaves analysed was not specified, however, and it should also be noted that this value was determined using picrate papers and reflectrometry, a less dependable method more sensitive to the presence of interfering substances (Brinker and Seigler, 1989).

Assessing the ecological significance of the range of cyanogenic glycoside concentrations recorded here is difficult. While the high concentrations in several species (e.g. >2 mg CN g^{-1} d. wt; Table 1) would almost certainly constitute toxic levels important in defence—plants with >600 μg HCN g^{-1} d. wt are considered potentially dangerous to livestock, for example (Haskins *et al*., 1987)—the ecological significance of lower concentrations (e.g. approx. 8–50 μg CN g^{-1} d. wt) is harder to determine. This reflects

the fact that despite the well-documented effectiveness of cyanogenesis in defence against generalist herbivores (e.g. Jones, 1998; Gleadow and Woodrow, 2002), overall there is no known particular concentration at which cyanogenic compounds are effective in herbivore deterrence. This is in part because unfortunately many herbivory studies only report the presence or absence of cyanogenesis, and not the actual concentrations of cyanogenic glycosides. Moreover, the efficacy of cyanogenesis as a defence depends not only on the concentration of cyanogenic glycosides, but also on the physiology, morphology and behaviour of the consumer (Gleadow and Woodrow, 2002).

Intra-plant variation in cyanogenic glycoside content

In tropical forests, it is estimated that up to 70 % of a leaf's lifetime damage occurs while expanding (Coley and Barone, 1996). This differential intensity of herbivory among old and young leaves, and the frequent observation that defence compounds tend to be concentrated in plant tissues of higher value to reproduction or growth (e.g. young leaves) is summarized in the Optimal Allocation Theory (OAT) of defence. This theory predicts that the most vulnerable and valuable plant parts—those susceptible to attack and most likely to contribute to growth and reproductive fitness such as reproductive structures and young leaves—will be more defended (McKey, 1974; Rhoades, 1979).

Results here add to the already substantial body of work on mostly temperate cyanogenic species consistent with the predictions of the OAT (e.g. Martin *et al*., 1938; Dement and Mooney, 1974; Cooper-Driver *et al*., 1977; Shore and Obrist, 1992; Dahler *et al*., 1995; Thomsen and Brimer, 1997; Gleadow *et al*., 1998; Gleadow and Woodrow, 2000*b*). In all species where young leaves were sampled, they contained significantly higher concentrations of cyanogenic glycosides than old leaves. This trend was most apparent in species that had low cyanogen content in old leaves (e.g. *C. sublimis*, *C. myrianthus*, *O. heterophylla* and *P. australiana*) (Table 1). Moreover, in some cases, individuals of these species appeared only to invest in cyanogenic glycoside defence in young leaves; acyanogenic old leaves were seemingly reliant more on physical toughness. Thus, leaf age is an important consideration when assigning the cyanogenic phenotype.

Again consistent with the OAT, reproductive tissues such as floral buds, flowers and fruits/seeds tended to have high total cyanogen content (Table 1). This pattern has been commonly reported among cyanogenic species (e.g. Spencer and Seigler, 1983; Selmar *et al*., 1991; Selmar, 1993*b*; Thomsen and Brimer, 1997; Webber, 1999). One notable exception to this was the low to negligible concentrations of cyanogenic glycosides in mature seeds of *C. sublimis*; unlike the fleshy seeds of many rainforest species, *C. sublimis* seeds are dry and papery. The absence of cyanogenesis in mature seeds of proteaceous *Grevillea* spp. was reported by Lamont (1993) in species with cyanogenic foliage and flowers. The higher concentrations in floral tissues of *C. sublimis* is consistent with previous reports for proteaceous species which tend to have high concentrations of cyanogenic glycosides in flowers, while leaves may have low total cyanogen content or be acyanogenic (e.g. Smith and White, 1918; Tjon Sie Fat, 1979*a*; Lamont, 1993).

Intra-population variation in cyanogenic glycoside content

All individuals of the majority of species were cyanogenic, albeit with low concentrations of cyanogenic glycosides in some instances. Negative results with FA papers for old leaves were only obtained for individuals of three of the 18 cyanogenic species. In the population of one of these species, *B. platynema*, 50 % of individuals were determined to be acyanogenic, with cyanogenic glycoside concentrations much less than the $8\ \mu g\ CN\ g^{-1}$ d. wt threshold. The two other exceptions were *C. myrianthus* and *P. australiana.* Unlike *B. platynema*, cyanogenesis in individuals of these species varied qualitatively with leaf age and plant part. Thus, assigning the acyanogenic phenotype in these species was problematic.

This developmental trend towards differences in expression of cyanogenic potential has been reported previously; cyanogenesis is known be affected by plant age, growth phase, as well as the plant part used (Jones, 1972; Gibbs, 1974; Seigler, 1991). Consequently, as noted earlier, studies have reported a greater frequency of cyanogenesis when testing reproductive tissues, young foliage and shoots compared with old leaves (e.g. Gibbs, 1974; Aikman *et al*., 1996; Thomsen and Brimer, 1997; Buhrmester *et al*., 2000; Mali and Borges, 2003). These findings emphasize the importance of only comparing leaves of a similar age when classifying individuals according to the presence or absence of cyanogenesis.

Aside from the three species mentioned above, no acyanogenic individuals were identified in populations of other cyanogenic species. While the small sample sizes for most species reduced the likelihood of encountering an acyanogenic individual, even within populations of the more abundant species such as *B. collina* (n = 46 all sites), *C. sublimis* (n = 31 at all sites) and *R. javanica* (n = 249; Webber, 1999), no acyanogenic individuals were detected. In the latter example, the quantitative screening of >800 individuals of *R. javanica* failed to detect an acyanogenic individual in several distinct populations (Webber, 2005). This number (800) was substantially greater than the number of individuals predicted by Gleadow and Woodrow (2000*a*) and Goodger *et al*. (2002) (n = 95–100) that would need to be sampled to capture an acyanogenic individual assuming a similar genetic system for cyanogenesis to *Trifolium repens* (Hughes *et al*., 1988) and an estimate of the rarity of a species (or polymorph) (McArdle, 1990). The floristic heterogeneity of the rainforest makes sampling large populations challenging; it is noteworthy, however, that others have detected polymorphism for cyanogenesis in tropical studies based on very small sample sizes (e.g. n = 2) (Kaplan *et al*., 1983; Thomsen and Brimer, 1997). These acyanogenic morphs, determined only by indicator paper tests in these studies, were not verified by quantitative assay as for *B. platynema* here.

Conclusions

In summary, the findings of this survey indicate that cyanogenesis is an important, yet little studied, chemical defence in tropical rainforests. The identification of specific cyanogens in but a few of the cyanogenic species first reported here has yielded novel findings. Given the large number of new reports for species belonging to plant families or orders in which cyanogenesis has been little reported, the ongoing characterization of cyanogenic constituents in these species will potentially be of both phytochemical and chemotaxonomic significance. In addition, preliminary data on intra-population variation in cyanogenesis here suggest that ontogenetic variation in cyanogenesis, and polymorphism for cyanogenesis merit further investigation in tropical rainforest species.

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APPENDIX

Summary of all species tested for cyanogenesis within $6 \times 200\,m^2$ plots at five sites in upland/highland (U) or lowland (L) tropical rainforest, on sites contrasting in soil type: basalt sites at Lamins Hill (B1) and Longlands Gap (B2), and sites on granite at Mt Nomico (G), on rhyolite at Longlands Gap (R) and on metamorphic substrate near Cape Tribulation (M). Species are listed in alphabetical order. Life forms: tree (T), shrub (SH), herb (H), vine (V), treefern (TF), palm (P) and hemi-epiphyte (HE). The results (+ or –) for tests using Feigl–Anger papers and approx. 1 g f. wt leaf tissue, with and without the addition of pectinase (+/– enz) for *n* individuals of each species are listed. All tests were carried out using most recently fully expanded leaves and in most instances also using young leaves. In some cases, leaf tips (tips), only a few fruit (ft) or flowers (flwr) were tested. Previous findings for species and in some cases genera are noted (e.g. Proteaceae species tested by E. E. Conn, University of California, Davis, CA, USA, pers. comm. based on herbarium specimens). Species included in phytochemical screenings of Queensland rainforest taxa (alkaloids, CN; Webb, 1948, Webb, 1949) are noted, most were not tested for CN (DNT). Canopy species or rare species for which no sample was obtained were included in floristic analysis, but were not tested for cyanogenesis (DNT). Lodgement numbers at Brisbane (BRI) and The University of Melbourne (MELU) herbaria are given.

Appendix

Lifeform	Species	Family	HCN +/– enz (*n* tested)	Upland/lowland	Site (substrate)	Previous reports	Lodgement no.
T	*Acacia celsa* Tindale	Mimosaceae	–/– (3)	U	R	Webb (1949) DNT	
T	*Acmena graveolens* (F.M.Bailey) L.S.Sm.	Myrtaceae	–/– (3)	L	M		MELU102318
T	*Acmena resa* B.Hyland	Myrtaceae	–/– (2)	U	B2, R		
T	*Acronychia acidula* F.Muell.	Rutaceae	–/– (2)	U	G	Webb (1949) DNT	
T	*Acronychia acronychioides* (F.Muell.) T.G.Hartley	Rutaceae	–/– (3)	U	G		
T	*Acronychia crassipetala* T.G.Hartley	Rutaceae	–/– (1)	U	B2		
SH	*Acronychia parviflora* C.T.White	Rutaceae	–/– (5)	U	B1, R		
SH	*Actephila* sp. (Wooroonooran NP *P.I.Forster+ PIF17151*)	Euphorbiaceae	–/– (5)	U	B1		
T	*Adenanthera pavonina* L.	Mimosaceae	–/– (1)	L	M		
T	*Agathis atropurpurea* B.Hyland	Araucariaceae	–/– (3)	U	R		
T	*Agathis microstachya* J.F.Bailey & C.T.White	Araucariaceae	–/– (1)	U	G		
T	*Agathis robusta* (C.Moore ex F.Muell.) F.M.Bailey	Araucariaceae	–/– (1)	U	B1		
SH	*Aglaia meridionalis* C.M.Pannell	Meliaceae	–/– (13)	U, L	B1, M		MELU102332
T	*Aglaia sapindina* (F.Muell.) Harms	Meliaceae	–/– (2)	L	M		
T	*Aglaia tomentosa* Teijsm. & Binn.	Meliaceae	–/– (5)	U, L	B1, B2, G, M		MELU102275
T	*Alangium villosum* subsp. *polyosmoides* (F.Muell.) Bloemb.	Alangiaceae	–/– (3)	U	B1	Webb (1949) DNT	MELU102329
T	*Alloxylon flammeum* P.H.Weston & Crisp	Proteaceae	–/– (2)	U	B2		
T	*Alloxylon wickhamii* (W.Hill ex F.Muell.) P.H.Weston & Crisp	Proteaceae	–/– (4)	U	G, B2		
H	*Alocasia brisbanensis* (F.M.Bailey) Domin‡	Araceae	+/+	U	B1	Hurst (1942)	
T	*Alphitonia whitei* Braid	Rhamnaceae	–/– (3)	U	G		MELU102103
H	*Alpinia arctiflora* (F.Muell.) Benth.	Zingiberaceae	–/– (1)	U	B1		
H	*Alpinia modesta* F.Muell. ex K.Schum.	Zingiberaceae	–/– (1)	U	B2		
T	*Alstonia scholaris* (L.) R.Br.	Apocynaceae	–/– (10)	L	M	Gibbs (1974) reported +CN; Webb (1949) DNT	BRI 578809, MELU102127, 102257
SH	*Alyxia ilicifolia* subsp. *ilicifolia* F.Muell.	Apocynaceae	–/– (3)	U	G		
V	*Alyxia spicata* R.Br.	Apocynaceae	–/– (2)	U	B1, R	Webb (1949) DNT	
T	*Antidesma erostre* F.Muell. ex Benth.	Euphorbiaceae	–/– (6)	U, L	B1, G, R, M		MELU102113
SH	*Antirhea* sp. (Mt Missery *L.W.Jessup+ GJD 3136*)	Rubiaceae	–/– (3)	U	B2		
T	*Antirhea tenuiflora* F.Muell. ex Benth.	Rubiaceae	–/– (4)	U, L	B1, G, M		
T	*Apodytes brachystylis* F.Muell.	Icacinaceae	–/– (6)	U	B1, G, R		MELU102188
T	*Archidendron ramiflorum* (F.Muell.) Kosterm.	Mimosaceae	–/– (4)	U, L	B1, M		
T	*Archidendron vaillantii* (F.Muell.) F.Muell.	Mimosaceae	–/– (3)	U	B2, G		MELU102186
T	*Archidendron whitei* I.C.Nielsen	Mimosaceae	–/– (1)	U	B1		
SH	*Ardisia bifaria* C.T.White & W.D.Francis	Myrsinaceae	–/– (2)	U	B1		
SH	*Ardisia brevipedata* F.Muell.	Myrsinaceae	–/– (7); frt –	U, L	B1, B2, G, R, M		MELU102148
T	*Argyrodendron* sp. (Boonjee *BH 2139RFK*)	Sterculiaceae	–/– (9)	U	B1		
T	*Arytera pauciflora* S.T.Reynolds	Sapindaceae	–/– (4)	U, L	B1, M		
SH	*Atractocarpus hirtus* (F.Muell.) Puttock	Rubiaceae	–/– (7)	U, L	B1, M	Webb (1949) DNT	
SH	*Atractocarpus merikin* (F.M.Bailey) Puttock	Rubiaceae	–/– (3)	U	B1, B2		
T	*Auranticarpa papyracea* L.Cayzer, Crisp & I.Telford	Pittosporaceae	–/– (2)	U	B2, G		
V	*Austrobaileya scandens* C.T.White	Austrobaileyaceae	–/– (6); flwr –	U	B1		
SH	*Austromatthaea elegans* L.S.Sm.	Monimiaceae	–/– (3)	U	G, R		
T	*Austromuellera trinervia* C.T.White	Proteaceae	–/– (4)	U, L	B1, M		
V	*Austrosteenisia stipularis* (C.T.White) Jessup	Fabaceae	–/– (4)	U	B1, G		

APPENDIX *Continued*

Lifeform	Species	Family	HCN +/– enz (*n* tested)	Upland/lowland	Site (substrate)	Previous reports	Lodgement no.
T	*Balanops australiana* F.Muell.	Balanopaceae	–/– (3)	U	R, G	Webb (1949) DNT	MELU102216, 102108
T	*Beilschmiedia bancroftii* (F.M. Bailey) C.T.White	Lauraceae	–/– (3)	U, L	B1, G, M	Webb (1949) DNT	MELU102219
T	*Beilschmiedia castrisinensis* B.Hyland	Lauraceae	–/– (2)	L	M		
T	*Beilschmiedia collina* B.Hyland	Lauraceae	+/+	U	B1, B2, G, R		BRI 578804, MELU102299, 102300
T	*Beilschmiedia oligandra* L.S.Sm.	Lauraceae	–/– (3)	U	G		
T	*Beilschmiedia recurva* B.Hyland	Lauraceae	–/– (4)	U	B1, G		
T	*Beilschmiedia tooram* (F.M.Bailey) B.Hyland	Lauraceae	–/– (10)	U	B1, B2, G		MELU102211
T	*Bobea myrtoides* (F.Muell.) Valeton	Rubiaceae	–/– (8)	U	G, R		MELU102105, 102110
SH	*Bowenia spectabilis* Hook. ex Hook.f.	Stangeriaceae	–/– (6)	U, L	B1, M		
T	*Brachychiton acerifolius* (A.Cunn. ex G.Don.) Macarthur	Sterculiaceae	–/– (3)	U, L	B2, M		
T	*Brackenridgea australiana* F.Muell.	Ochnaceae	–/– (4)	U, L	G, R, M		MELU102322
SH/T	*Breynia cernua* (Poir.) Muell.Arg	Euphorbiaceae	–/– (2)	U	B2, G	Webb (1949) 1948 *B. oblongifolia* Muell. Arg. +CN	
T	*Brombya platynema* F.Muell.	Rutaceae	+/+	L	M	Webb (1949) DNT	BRI 578818. MELU102283, 102313
T	*Bubbia semecarpoides* (F.Muell.) B.L.Burtt	Winteraceae	–/– (5)	U	B1, G		
V (P)	*Calamus australis* Mart.	Arecaceae	–/– (1);	U	B1		
V	*Calamus moti* F.M.Bailey	Arecaceae	–/– (1)	U	B1		
T	*Caldcluvia australiensis* (Schltr.) Hoogland	Cunoniaceae	–/– (1)	U	B1		
T	*Calophyllum costatum* F.M.Bailey	Clusiaceae	–/– (3)	U	B2, R		
T	*Cananga odorata* (Lam.) Hook.f. & Thomson	Annonaceae	–/– (2)	L	M		
T	*Canarium muelleri* F.M.Bailey	Burseraceae	–/– (1)	U	G		MELU102250
T	*Canthium* sp.	Rubiaceae	–/– (1)	U	G		
T	*Carallia brachiata* (Lour.) Merr.	Rhizophoraceae	–/– (1)	L	M		
T	*Cardwellia sublimis* F.Muell.	Proteaceae	+/+	U, L	B1, B2, G, R, M	E. E. Conn (pers. comm.) 1 of 7 +ve	BRI 578806, MELU102280, 102281
T	*Carnarvonia araliifolia* var. *montana* B.Hyland	Proteaceae	–/– (3)	U	B2, G, R	E. E. Conn (pers. comm.) –ve	MELU102282
V	*Carronia protensa* (F.Muell.) Diels	Menispermaceae	–/– (5)	U, L	B1, B2, M		MELU102213
T	*Casearia costulata* L.W.Jessup	Salicaceae†	–/– (4)	U	B1, B2, G, R	Webb (1949) DNT	
T	*Casearia dallachii* F.Muell.	Salicaceae†	–/– (1)	L	M		
T	*Casearia grayi* L.W.Jessup	Salicaceae†	–/– (2) dry*	U	B2		
T	*Castanospermum australe* A.Cunn. & C.Fraser ex Hook.	Fabaceae	–/– (3)	L	M	Webb (1949) DNT	
T	*Castanospora alphandii* (F.Muell.) F.Muell.	Sapindaceae	–/– (3)	U	B1, B2		MELU102130
V	*Cayratia saponaria* (Seem. & Benth.) Domin	Vitaceae	–/– (1)	L	M	*C. acris* Gibbs (1974) –CN	
T	*Celtis paniculata* (Endl.) Planch.	Ulmaceae	–/– (1)	L	M		
V	*Cephalaralia cephalobotrys* (F.Muell.) Harms	Araliaceae	–/– (2)	U	B1, B2		
T	*Ceratopetalum succirubrum* C.T.White	Cunoniaceae	–/– (4)	U	B2, G	Webb (1949) DNT	
T	*Cerbera floribunda* K.Schum.	Apocynaceae	–/– (1)	U, L	G, M	Webb (1949) DNT	
T	*Chionanthus axillaris* R.Br.	Oleaceae	–/– (4)	U	B1, G		MELU102327
T	*Cinnamomum laubatii* F.Muell.	Lauraceae	–/– (3)	U	B1, G, R	Webb (1949) DNT	MELU102210
V	*Cissus hypoglauca* A.Gray	Vitaceae	–/– (2)	U	G		
V	*Cissus penninervis* (F.Muell.) Planch.	Vitaceae	–/– (1)	U, L	R, M		

V	*Cissus sterculiifolia* (F.Muell. ex Benth.) Planch.	Vitaceae	–/– (4)	U	B1, B2, G		MELU102325
V	*Cissus vinosa* Jackes	Vitaceae	–/– (3)	U	B1, B2, G		MELU102195
T	*Citronella smythii* (F.Muell.) R.A.Howard	Icacinaceae	–/– (4)	U, L	B1, G, M		MELU102143
T	*Claoxylon tenerifolium* (Baill.) F.Muell.	Euphorbiaceae	–/– (1)	U	B1		
T	*Cleistanthus myrianthus* (Hassk.) Kurz	Euphorbiaceae	+/+	L	M		BRI 578811, MELU102122, 102123, 102258
T	*Clerodendrum grayi* Munir	Verbenaceae	+/+	U	B1, B2, G	Other *Clerodendrum* spp. +CN (Gibbs, 1974; Tjon Sie Fat, 1979*a*; Adsersen *et al.*, 1988)	BRI 578815, MELU102115, 102116, 102117
T	*Cnesmocarpon dasyantha* (Radlk.) Adema	Sapindaceae	–/– (2)	U	G		
V	*Connarus conchocarpus* F.Muell.	Connaraceae	–/– (1)	L	M		
SH	*Cordyline petiolaris* (Domin) Pedley	Laxmanniaceae	–/– (2)	U	B1		
SH	*Cordyline* sp.	Laxmanniaceae	–/– (1)	U	G		
T	*Corynocarpus cribbianus* (F.M.Bailey) L.S.Sm.	Corynocarpaceae	–/– (1)	U	B1	*C. laevigata* +CN (Webb, 1948)	
SH	*Crispiloba disperma* (S.Moore) Steenis	Alseuosmiaceae	–/– (4)	U	G		
T	*Cryptocarya angulata* C.T.White	Lauraceae	–/– (4)	U	B1, G, R		MELU102102
T	*Cryptocarya cocosoides* B.Hyland	Lauraceae	–/– (3)	U	B2, G		MELU102157, 102268
T	*Cryptocarya corrugata* C.T.White & W.D.Francis	Lauraceae	–/– (3)	U	B1, B2, G, R		MELU102147
T	*Cryptocarya densiflora* Blume	Lauraceae	–/– (2)	U	G, R		MELU102104, 102269
T	*Cryptocarya grandis* B.Hyland	Lauraceae	–/– (3);	U, L	B1, B2, G, M		MELU102247
T	*Cryptocarya hypospodia* F.Muell.	Lauraceae	–/– (1)	L	M		
T	*Cryptocarya laevigata* Blume	Lauraceae	–/– (2)	U, L	G, M		
T	*Cryptocarya leucophylla* B.Hyland	Lauraceae	–/– (1)	U	B2, R		MELU102248
T	*Cryptocarya lividula* B.Hyland	Lauraceae	–/– (2)	U	G, R		MELU102095
T	*Cryptocarya mackinnoniana* F.Muell.	Lauraceae	–/– (5)	U, L	B1, G, M		MELU102212
T	*Cryptocarya melanocarpa* B.Hyland	Lauraceae	–/– (5)	U	B1, B2		
T	*Cryptocarya murrayi* F.Muell.	Lauraceae	–/– (2)	U, L	B1, M		
T	*Cryptocarya oblata* F.M.Bailey	Lauraceae	–/– (2)	U, L	B1, M	Webb (1949) DNT	MELU102099
T	*Cryptocarya pleurosperma* C.T.White & W.D.Francis	Lauraceae	–/– (4)	U	B1, G	Webb (1949) DNT	MELU102270
T	*Cryptocarya putida* B.Hyland	Lauraceae	–/– (4)	U	G, R		MELU102144
T	*Cryptocarya saccharata* B.Hyland	Lauraceae	–/– (3)	U	B2, R		
T	*Cryptocarya smaragdina* B.Hyland	Lauraceae	–/– (3)	U	B2, R		MELU102193
T	*Cupaniopsis flagelliformis* (F.M.Bailey) Radlk. var. *flagelliformis*	Sapindaceae	–/– (4)	U	B1		MELU102129
T	*Cupaniopsis* sp.	Sapindaceae	–/– (1)	L	M		
TF	*Cyathea rebeccae* (F.Muell.) Domin	Cyatheaceae	–/– (2)	U	G, R		
T	*Cyclophyllum multiflorum* S.T.Reynolds & R.J.F.Hend.	Rubiaceae	–/– (1)	U	B1	*Canthium vaccinifolium* F. Muell. +CN Webb (1949) 1948	
T	*Daphnandra repandula* (F.Muell.) F.Muell.	Monimiaceae	–/– (2)	U	B1, B2, G		
T	*Darlingia darlingiana* (F.Muell.) L.A.S.Johnson	Proteaceae	–/– (2)	U	G	E. E. Conn (pers. comm.) –ve	
T	*Darlingia ferruginea* J.F.Bailey	Proteaceae	–/– (3)–	U	B1, B2	E. E. Conn (pers. comm.) –ve	
T	*Davidsonia pruriens* F.Muell.	Davidsoniaceae	–/– (2)	U	G	Webb (1949) DNT; +CN (Rosenthaler, 1929; Hurst, 1942); –CN Gibbs (1974)	MELU102151, 102152
T	*Decaspermum* humile (G.Don.) A.J.Scott	Myrtaceae	–/– (1) dry*	L	M		
T	*Delarbrea michieana* (F.Muell.) F.Muell.	Araliaceae	–/– (4)	U	B1, G		
V	*Dendrotrophe varians* (Blume) Miq.	Santalaceae	–/– (1)	U	R		
V	*Derris* sp. (Daintree *D.E. Boyland+469*)	Fabaceae	–/– (1) dry*	L	M		

APPENDIX *Continued*

Lifeform	Species	Family	HCN +/– enz (*n* tested)	Upland/lowland	Site (substrate)	Previous reports	Lodgement no.
V	*Desmos goezeanus* (F.Muell.) Jessup	Annonaceae	–/– (2)	U	G		
V	*Dichapetalum papuanum* (Becc.) Boerl.	Dichapetalaceae	–/– (4)	U	B1		MELU102326
T	*Dinosperma stipitatum* (C.T.White & W.D.Francis) T.G. Hartley	Rutaceae	–/– (3)	U	B1		
T	*Diospyros cupulosa* F.Muell.	Ebenaceae	–/– (1)	L	M		
T	*Diospyros hebecarpa* A.Cunn. ex Benth.	Ebenaceae	–/– (1) dry*	U	B1		MELU102307
T	*Diploglottis bernieana* S.T.Reynolds	Sapindaceae	–/– (2)	L	M		
T	*Diploglottis bracteata* Leenh.	Sapindaceae	–/– (1)	U	G		
T	*Doryphora aromatica* (F.M.Bailey) L.S.Sm.	Monimiaceae	–/– (5)	U, L	B1, B2, M	Webb (1949) DNT	
T	*Dysoxylum alliaceum* Blume (Blume)	Meliaceae	–/– (1)	L	M		
T	*Dysoxylum arborescens* (Blume) Miq.	Meliaceae	–/– (2)	U, L	B1, M		
T	*Dysoxylum klanderi* F.Muell.	Meliaceae	–/– (3)	U	B1, B2, R		
T	*Dysoxylum oppositifolium* F.Muell.	Meliaceae	–/– (3)	U	B2, G		MELU102273
T	*Elaeocarpus bancroftii* F.Muell. & F.M.Bailey	Elaeocarpaceae	–/– (3)	L	M		
T	*Elaeocarpus eumundi* F.M.Bailey	Elaeocarpaceae	–/– (1)	U	G, R		MELU102125
T	*Elaeocarpus foveolatus* F.Muell.	Elaeocarpaceae	–/– (2)	U	B1, R		
T	*Elaeocarpus grahamii* F.Muell.	Elaeocarpaceae	–/– (1)	L	M		
T	*Elaeocarpus largiflorens* C.T.White subsp. *largiflorens*	Elaeocarpaceae	–/– (4)	U	B1, G		
T	*Elaeocarpus ruminatus* F.Muell.	Elaeocarpaceae	–/– (3)	U	B2, G		
T	*Elaeocarpus sericopetalus* F.Muell.	Elaeocarpaceae	+/+	U	G, R		BRI 578817, MELU102135, 102304
T	*Elaeocarpus* sp. (Mt Bellenden Ker *LJB 18336*)	Elaeocarpaceae	–/– (3)	U	B2, G, R		MELU102304
V	*Embelia caulialata* S.T.Reynolds	Myrsinaceae	–/– (1) dry*	L	M		
V	*Embelia grayi* S.T.Reynolds	Myrsinaceae	+/+	U	B1, B2		BRI 578803, MELU102267
T	*Endiandra bessaphila* B.Hyland	Lauraceae	–/– (2)	U	B1		
T	*Endiandra dielsiana* Teschn.	Lauraceae	–/– (2)	U	G		
T	*Endiandra hypotephra* F.Muell.	Lauraceae	DNT	L	M		
T	*Endiandra leptodendron* B.Hyland	Lauraceae	–/– (7)	U, L	B1, M		MELU102293
T	*Endiandra microneura* C.T.White	Lauraceae	–/– (3)	L	M		
T	*Endiandra monothyra* B.Hyland subsp. *monothyra*	Lauraceae	–/– (3)	U	B1, B2		
T	*Endiandra montana* C.T.White	Lauraceae	DNT	U	B2		
T	*Endiandra palmerstonii* (F.M.Bailey) C.T.White & W.D.Francis	Lauraceae	–/– (2)	U	B2, G	Webb (1949) DNT	MELU102294
T	*Endiandra sankeyana* F.M.Bailey	Lauraceae	–/– (3)	U	B1, B2		MELU102155
T	*Endiandra sideroxylon* B.Hyland	Lauraceae	–/– (3)	U	B2		MELU102109
T	*Endiandra wolfei* B.Hyland	Lauraceae	–/– (3); sht –	U	B1, G		MELU102295
T	*Endospermum myrmecophilum* L.S.Sm.	Euphorbiaceae	–/– (1) dry *	L	M		
V	*Entada phaseoloides* (L.) Merr.	Mimosaceae	–/– (1)	L	M		
HE	*Epipremnum pinnatum* (L.) Engl.	Araceae	–/– (2)	L	M		
V	*Erycibe coccinea* (F.M.Bailey) Hoogl.	Convolvulaceae	–/– (3)	L	M		
T	*Erythroxylum ecarinatum* Burck ex Hoch.	Erythroxylaceae	–/– (2)	U	B1	Webb (1949) DNT	MELU102225
SH	*Eupomatia barbata* Jessup	Eupomatiaceae	–/– (2) dry*	U, L	B1, M		
SH/T	*Eupomatia laurina* R.Br.	Eupomatiaceae	–/– (4)	U	B2, G	Gibbs (1974) 'doubtfully cyanogenic'; Webb (1949) DNT	MELU102331
V	*Eustrephus latifolius* R.Br. ex Ker Gawl.	Philesiaceae	–/– (2)	U, L	B1, M		
T	*Fagraea cambagei* Domin	Gentianaceae	–/– (4)	L	M		MELU102317

T	*Fagraea fagraeacea* (F.Muell.) Druce	Gentianaceae	–/– (3)	U	B1, B2, G, R		MELU102323
T	*Ficus congesta* Roxb.	Moraceae	–/– (1)	L	M		
T	*Ficus crassipes* F.M.Bailey	Moraceae	–/– (1)	U	B1		
T	*Ficus destruens* F.Muell. ex C.T.White	Moraceae	–/– (1)	U	B2, G		
T	*Ficus leptoclada* Benth.	Moraceae	DNT	U	B1, B2		MELU102107
V	*Ficus pantoniana* King	Moraceae	–/– (1)	L	M		
T	*Ficus pleurocarpa* F.Muell.	Moraceae	–/– (1)	U	B1		
T	*Ficus triradiata* Corner	Moraceae	–/– (1)	L	M		
V	*Flagellaria indica* L.	Flagellariaceae	+/+	U, L	B1, G, M	+CN (1912)	BRI 578816, MELU102259, 102296
T	*Flindersia bourjotiana* F.Muell.	Rutaceae	–/– (4)	U, L	B2, G, R, M	Webb (1949) DNT	
T	*Flindersia brayleyana* F.Muell.	Rutaceae	–/– (1)	U	B2	Webb (1949) DNT	
T	*Flindersia laevicarpa* C.T.White & W.D.Francis	Rutaceae	–/– (2)	U	G		MELU102222
T	*Flindersia pimenteliana* F.Muell.	Rutaceae	–/– (2)	U	G, R	Webb (1949) DNT	MELU102132, 102106
T	*Fontainea picrosperma* C.T.White	Euphorbiaceae	–/– (2)	U	B2		
T	*Franciscodendron laurifolium* (F.Muell.) B.Hyland & Steenis	Sterculiaceae	–/– (10)	U	B1, G		
V	*Freycinetia excelsa* F.Muell.	Pandanaceae	–/– (3)	U	B1, B2		
V	*Freycinetia scandens* Gaudich.	Pandanaceae	–/– (1)	U	B1		
T	*Galbulimima baccata* F.M.Bailey	Himantandraceae	–/– (3)	U	B1, B2, G, R	Webb (1949) DNT; fruits –CN (Bailey, 1909 in Webb, 1948)	
T	*Garcinia gibbsiae* S.Moore	Clusiaceae	–/– (7)	U	B1		MELU102126
T	*Garcinia warrenii* F.Muell.	Clusiaceae	–/– (4)	L	M		
T	*Gardenia ovularis* F.M.Bailey	Rubiaceae	–/– (5)	U, L	G, M	Webb (1949) DNT	MELU102319
T	*Gevuina bleasdalei* (F.Muell.) Sleumer	Proteaceae	–/– (3)	U	B1, G	E. E. Conn (pers. comm.) –ve	MELU102292
T	*Gillbeea adenopetala* F.Muell.	Cunoniaceae	–/– (3)	U	B1, G		
T	*Glochidion harveyanum* Domin var. *harveyanum*	Euphorbiaceae	–/– (1)	U	G	Webb (1949) DNT	
T	*Glochidion hylandii* Airy Shaw	Euphorbiaceae	–/– (1)	U	B2, G	Webb (1949) DNT	
T	*Gmelina fasciculiflora* Benth.	Lamiaceae	–/– (2)	U, L	G, M	Webb (1949) DNT	MELU102261, 102262,102263
T	*Gomphandra australiana* F.Muell.	Icacinaceae	–/– (2)	L	M		MELU102333
T	*Goniothalamus australis* Jessup	Annonaceae	–/– (6)	U	B1		MELU102185, 102290
T	*Gossia dallachiana* (F.Muell.) N.Snow & Guymer	Myrtaceae	–/– (5)	U	B1, B2, G		MELU102220
T	*Gossia myrsinocarpa* (F.Muell.) N.Snow & Guymer	Myrtaceae	–/– (1)	U	B2		
T	*Gossia grayii* N.Snow & Guymer	Myrtaceae	–/– (2)	U	G		MELU102146
T	*Grevillea baileyana* McGill.	Proteaceae	–/– (1)	L	M	Webb (1952); Hurst (1942) *Grevillea* spp. +CN; E. E. Conn (pers. comm.) –ve	
T	*Guioa acutifolia* Radlk.	Sapindaceae	–/– (2)	U, L	B2, M		
T	*Guioa lasioneura* Radlk.	Sapindaceae	–/– (2)	U	B1, G		
T	*Guioa montana* C.T.White	Sapindaceae	–/– (2)	U	R		MELU102150
SH	*Gymnostachys anceps* R.Br.	Araceae	–/– (2)	U, L	B2, M		
V	*Gynochtodes* sp. (Lamb Range *J.W.398*)	Rubiaceae	–/– (2)	U	G, R		
T	*Halfordia kendack* (Montrouz.) Guillaumin	Rutaceae	–/– (3)	U	B1, B2, G, R	Webb (1949) DNT	MELU102112
SH	*Haplostichanthus* sp. (Coopers Creek *B. Gray 2433*)	Annonaceae	–/– (7)	L	M		MELU102291
SH	*Haplostichanthus* sp. (Topaz *L.W.Jessup 520*)	Annonaceae	–/– (7)	U	B1		MELU102328
SH	*Harpullia frutescens* F.M.Bailey	Sapindaceae	–/– (1)	U	B2		
SH/T	*Harpullia rhyticarpa* C.T.White & W.D.Francis	Sapindaceae	–/– (10)	U, L	B1, G, M	Webb (1949) DNT	
T	*Hedycarya loxocarya* (Benth.) W.D.Francis	Monimiaceae	–/– (4)	U	G		

APPENDIX *Continued*

Lifeform	Species	Family	HCN +/– enz (*n* tested)	Upland/lowland	Site (substrate)	Previous reports	Lodgement no.
T	*Helicia australasica* F.Muell.	Proteaceae	+/+	L	M	E. E. Conn (pers. comm.) flwr +ve; *H. robusta* +CN Pammel, 1911 in Webb (1949) 1948; Gibbs (1974)	BRI 578805, MELU102284
T	*Helicia blakei* Foreman	Proteaceae	+/+	U	B1	E. E. Conn (pers. comm.) –ve	BRI 578807, MELU102285
T	*Helicia lamingtoniana* (F.M.Bailey) C.T.White ex L.S.Sm.	Proteaceae	–/– (3)	U	B2	E. E. Conn (pers. comm.) –ve	MELU102214
T	*Hernandia albiflora* (C.T.White) Kubitzki	Hernandiaceae	–/– (4)	L	M	Webb (1949) DNT	MELU102314
V	*Hibbertia scandens* (Willd.) Dryand.	Dilleniaceae	–/– (1)	U	R		
V	*Hippocratea barbata* F.Muell.	Celastraceae	–/– (4)	U, L	B1, M		
V	*Hoya* sp.	Asclepiadaceae	–/– (1)	L	M		
T	*Hylandia dockrillii* Airy Shaw	Euphorbiaceae	–/– (2)	U	B1		
V	*Hypserpa decumbens* (Benth.) Diels	Menispermaceae	–/– (4)	U	B1, G		MELU102316
V	*Hypserpa laurina* (F.Muell.) Diels	Menispermaceae	–/– (2)	L	M	Webb (1949) DNT	MELU102276
V	*Hypserpa smilacifolia* Diels	Menispermaceae	–/– (1)	U	B2		
T	*Hypsophila dielsiana* Loes.	Celastraceae	–/– (3)	U	B1		MELU102311
T	*Irvingbaileya australis* (C.T.White) R.A.Howard	Icacinaceae	–/– (2)	U	B1, G		MELU102324
T	*Ixora biflora* Fosberg	Rubiaceae	–/– (2)	L	M		
T	*Ixora* sp. (North Mary LA *B.P.Hyland 8618*)	Rubiaceae	–/– (3)	U	B1, B2		
V	*Jasminum didymum* G.Forst.	Oleaceae	–/– (2)	U	B1, B2, G		
V	*Jasminum kajewskii* C.T.White	Oleaceae	–/– (2)	U	B2, G		
SH	*Lasianthus strigosus* Wight	Rubiaceae	–/– (2)	L	M		
SH/T	*Leea indica* (Burm.f.) Merr.	Leeaceae	–/– (1)	L	M		
SH/T	*Lepidozamia hopei* (W.Hill) Regel	Zamiaceae	–/– (3)	L	M		
T	*Lethedon setosa* (C.T.White) Kosterm.	Thymelaeaceae	–/– (2)	U	G		
P(T)	*Licuala ramsayi* (F.Muell.) Domin	Arecaceae	–/– (3)	L	M		
P(SH)	*Linospadix minor* (W.Hill) F.Muell.	Arecaceae	–/– (2)	L	M		
T	*Litsea bindoniana* F.Muell. (F.Muell.)	Lauraceae	–/– (2)	U	G		MELU102097
T	*Litsea connorsii* B.Hyland	Lauraceae	–/– (2)	U	G, R		
T	*Litsea leefeana* (F.Muell.) Merr.	Lauraceae	–/– (7)	U,L	B1, B2, M		MELU102145
T	*Loganiaceae* sp.	Loganiaceae	–/– (1)	U	G		
T	*Lomatia fraxinifolia* F.Muell. ex Benth.	Proteaceae	–/– (2)	U	B2, G	E. E. (Conn (pers. comm.) –ve; *L. silaifolia* R.Br. ft, flwr +CN Webb (1949) 1948	MELU102091
T	*Macaranga inamoena* F.Muell. ex Benth.	Euphorbiaceae	–/– (7)	U	B1	Webb (1949) DNT	MELU102156
T	*Macaranga subdentata* Benth	Euphorbiaceae	–/– (1)	L	M		
SH	*Mackinlaya confusa* Hemsl.	Araliaceae	–/– (1)	U	R		
SH	*Mackinlaya macrosciadea* (F.Muell.) F.Muell.	Araliaceae	–/– (4)	U	B1, G	Webb (1949) DNT	
V	*Maesa dependens* F.Muell.	Myrsinaceae	–/– (1)	U	R		
SH/T	*Melicope broadbentiana* F.M.Bailey	Rutaceae	–/– (3)	U	B1, G		MELU102131
T	*Melicope jonesii* T.G.Hartley	Rutaceae	–/– (1)	U	B2		
T	*Melicope vitiflora* (F.Muell.) T.G.Hartley	Rubiaceae	–/– (1)	U, L	B1, G, M		
V	*Melodinus acutiflorus* F.Muell.	Apocynaceae	–/– (1)	L	M	Webb (1949) DNT	
V	*Melodinus australis* (F.Muell.) Pierre	Apocynaceae	–/– (4)	U	B1, G, R		
V	*Melodinus baccellianus* (F.Muell.) S.T.Blake	Apocynaceae	–/– (3)	U	B1, B2		MELU102230
V	*Melodorum uhrii* F.Muell.	Annonaceae	–/– (1) dry*	L	M		
T	*Mischarytera lautereriana* (F.M.Bailey) H.Turner	Sapindaceae	–/– (2)	U	B2, G, R		MELU102286

T	*Mischocarpus exangulatus* (F.Muell.) Radlk.	Sapindaceae	+/+	U	B1		BRI 578801, MELU102190, 102288
T	*Mischocarpus grandissimus* (F.Muell.) Radlk.	Sapindaceae	+/+	U, L	G, M		BRI 578802, MELU102287
T	*Mischocarpus lachnocarpus* (F.Muell.) Radlk.	Sapindaceae	–/– (3)	U	B2, G		
T	*Mischocarpus macrocarpus* S.T.Reynolds	Sapindaceae	–/– (3)	U	B1, B2		
T	*Mischocarpus pyriformis* (F.Muell.) Radlk. subsp. *pyriformis*	Sapindaceae	–/– (1)	U	B2		
T	Monimiaceae Gen.(AQ63687) sp. (Davies Creek *L.J.Webb+ 6430*)	Monimiaceae	–/– (3)	U	B2, R		
V	*Morinda* Gen.(AQ124851) sp. (Boonjie *L.J.Webb+ 6837A*)	Rubiaceae	–/– (3)	U	B1		
V	*Morinda jasminoides* A.Cunn. ex Hook.	Rubiaceae	–/– (1)	U	B2, G	Webb (1949)–CN	
V	*Morinda* sp.	Rubiaceae	–/– (1)	U	G		
V	*Morinda umbellata* L.	Rubiaceae	–/– (1)	U	G		
T	*Musgravea heterophylla* L.S.Sm.	Proteaceae	–/– (2)	L	M	E. E. Conn (pers. comm.) 1 of 8 +ve	
T	*Musgravea stenostachya* F.Muell.	Proteaceae	–/– (4)	U	G, R	E. E. Conn (pers. comm.) –ve	
T	*Myristica globosa* subsp. *muelleri* (Warb.) W.J.de Wilde	Myristicaceae	–/– (3)	U	B1		
T	*Myristica insipida* R.Br.	Myristicaceae	–/– (3)	L	M		MELU102312
T	*Neisosperma poweri* (F.M.Bailey) Fosberg & Sachet	Apocynaceae	–/– (2)	U	B2		
T	*Neolitsea dealbata* (R.Br.) Merr.	Lauraceae	–/– (4)	U	B1, B2	Gibbs (1974) –CN	
V	*Neosepicaea jucunda* (F.Muell.) Steenis	Bignoniaceae	–/– (2)	L	M		
T	*Niemeyera prunifera* (F.Muell.) F.Muell.	Sapotaceae	–/– (4)	U, L	B1, G, M		MELU102149
P(T)	*Normanbya normanbyi* (W.Hill) L.H.Bailey	Arecaceae	–/–(4)	L	M		
T	*Opisthiolepis heterophylla* L.S.Sm.	Proteaceae	+/+	U	B1, B2	E.E . Conn (pers. comm.) flwr and lf +ve	BRI 578808, MELU102298
P(T)	*Oraniopsis appendiculata* (F.M.Bailey) J.Dransf., A.K.Irvine & N.W.Uhl	Arecaceae	–/– (1)	U	B1		
V	*Pachygone longifolia* F.M.Bailey	Menispermaceae	–/– (2)	L	M		
T	*Palaquium galactoxylon* (F.Muell.) H.J.Lam	Sapotaceae	–/– (1) dry*	L	M		
V	*Palmeria scandens* F.Muell.	Monimiaceae	–/– (4)	U	G		MELU102194
SH/T	*Pandanus monticola* F.Muell.	Pandanaceae	–/– (1)	U	G		
V	*Pandorea pandorana* (Andrews) Steenis	Bignoniaceae	–/– (1)	U	B2	Webb (1949) DNT	
V	*Pararistolochia australopithecurus* (F.Muell.) Michael J.Parsons	Aristolochiaceae	–/– (3)	U	B1, B2, G		
V	*Parsonsia latifolia* (Benth.) S.T.Blake	Apocynaceae	+/+	U	B1, G, R	Webb (1949) DNT; other *Parsonsia* spp. –CN	BRI 578800, MELU102128
V	*Parsonsia* sp. 1	Apocynaceae	–/– (1)	U	G		
V	*Parsonsia langiana* F.Muell	Apocynaceae	–/– (1)	U	R		
V	*Passiflora* sp. (Kuranda *BH12896*)	Passifloraceae	+/+	L	M		BRI 578813, MELU102297
T	*Perrottetia arborescens* (F.Muell.) Loes.	Celastraceae	–/– (1)	U	G		
SH/T	*Pilidiostigma papuanum* (Lauterb.) A.J.Scott	Myrtaceae	–/– (3)	L	M		
SH	*Pilidiostigma tetramerum* L.S.Sm.	Myrtaceae	–/– (4)	U	B1		MELU102274
T	*Pilidiostigma tropicum* L.S.Sm.	Myrtaceae	–/– (2)	U	B1		
V	*Piper caninum* Blume	Piperaceae	–/– (3)	L	M		MELU102265
V	*Piper novae-hollandiae* Miq.	Piperaceae	–/– (3)	U	B1, G	Webb (1949) DNT	
T	*Pitaviaster haplophyllus* (F.Muell.) T.G.Hartley	Rutaceae	–/– (12)	U, L	B1, G, M		MELU102100, 102187

APPENDIX *Continued*

Lifeform	Species	Family	HCN +/– enz (*n* tested)	Upland/lowland	Site (substrate)	Previous reports	Lodgement no.
SH/T	*Pittosporum rubiginosum* A.Cunn.	Pittosporaceae	–/– (3)	U, L	B1, B2, G, R, M	*P. undulatum* (Bailey, 1909 in Webb, 1949) 1948	MELU102192
T	*Pittosporum wingii* F.Muell.	Pittosporaceae	–/– (2)	U	G		
T	*Placospermum coriaceum* C.T.White & W.D.Francis	Proteaceae	–/– (2)	U	G		
T	*Podocarpus dispermus* C.T.White	Podocarpaceae	–/– (2)	U	B1		
T	*Polyalthia michaelii* C.T.White	Annonaceae	DNT	U	B1		
T	*Polyosma alangiacea* F.Muell.	Grossulariaceae	–/– (3)	U	G, R		
T	*Polyosma hirsuta* C.T.White	Grossulariaceae	–/– (1)	U	B1, B2		
T	*Polyosma rhytophloia* C.T.White & W.D.Francis	Grossulariaceae	–/– (1)	U	B2, R	Webb (1949) DNT	
T	*Polyosma rigidiuscula* F.Muell. & F.M.Bailey ex F.M. Bailey	Grossulariaceae	–/– (3)	U	B1		
T	*Polyscias australiana* (F.Muell.) Philipson	Araliaceae	+/+	U, L	B1, B2, G, R, M		BRI 578812, MELU102301
T	*Polyscias mollis* (Benth.) Harms & C.T.White	Araliaceae	–/– (1)	U	B1		
T	*Polyscias murrayi* (F.Muell.) Harms	Araliaceae	–/– (1)	U	B1	Webb (1949) DNT	
SH	*Polyscias purpurea* C.T.White	Araliaceae	–/– (4)	U	G		MELU102154
HE	*Pothos longipes* Schott	Araceae	–/– (4)	U, L	B1, M		
T	*Pouteria asterocarpon* (P.Royen) Jessup	Sapotaceae	–/– (1)	U	B2		
T	*Pouteria brownlessiana* (F.Muell.) Baehni	Sapotaceae	–/– (3)	U, L	B1, B2, G, M		
T	*Pouteria castanosperma* (C.T.White) Baehni	Sapotaceae	–/– (4)	U	B1, G		
T	*Pouteria chartacea* (F.Muell. ex Benth.) Baehni	Sapotaceae	–/– (3) 2 dry*	L	M		
T	*Pouteria myrsinodendron* (F.Muell.) Jessup	Sapotaceae	–/– (7)	U, L	G, M		MELU102221
T	*Pouteria papyracea* (P.Royen) Baehni	Sapotaceae	–/– (2)	U	B2		MELU102308, 102309
T	*Pouteria pearsoniorum* Jessup	Sapotaceae	–/– (1)	U	R		
T	*Prunus turneriana* (F.M.Bailey) Kalkman	Rosaceae	+/+	U, L	B1, M		BRI 578814, MELU102133, 102134
H	*Pseuderanthemum variabile* (R.Br.) Radlk.	Acanthaceae	–/– (1)	L	M	Webb (1949) DNT	
T	*Pseuduvaria froggattii* (F.Muell.) Jessup	Annonaceae	–/– (3)	L	M		MELU102310
T	*Pseuduvaria mulgraveana* Jessup var. *glabrescens*	Annonaceae	–/– (1)	U	G		
SH	*Psychotria dallachiana* Benth.	Sapindaceae	–/– (1)	U	B2		
SH	*Psychotria loniceroides* Sieber ex DC.	Rubiaceae	–/– (2)	U	G	Webb (1949) DNT	
SH	*Psychotria nematopoda* F.Muell.	Rubiaceae	–/– (2)	L	M		
SH	*Psychotria* sp.	Rubiaceae	–/– (1)	L	M		
SH	*Psychotria* sp. (Utchee Creek H. *Flecker NQNC 5313*)	Rubiaceae	–/– (3)	U	G		
SH	*Psychotria submontana* Domin	Rubiaceae	–/– (2)	U	B1, G		
T	*Psydrax laxiflorens S.T.Reynolds & R.J.F.Hend.*	Rubiaceae	–/– (2)	U	G		
T	*Pullea stutzeri* (F.Muell.) Gibbs	Cunoniaceae	–/– (3)	U	G		
SH	*Randia* sp. (Boonjie *L.W.Jessup+ GJM264*)	Rubiaceae	–/– (1)	U	B1		
SH	*Randia tuberculosa* F.M.Bailey	Rubiaceae	–/– (7)	U	B1, G		MELU102158
T	*Rapanea achradifolia* (F.Muell.) Mez	Myrsinaceae	–/– (3)	U	B2, G, R		MELU102217
SH/T	*Rapanea porosa* (F.Muell.) Mez	Myrsinaceae	–/– (3)	U, L	R, M		
SH	*Rapanea* sp. (Atherton *K.J.White AQ91778*)	Myrsinaceae	–/– (2)	U	R		MELU102260
HE	*Rhaphidophora petrieana* A.Hay	Araceae	–/– (3)	L	M	Webb (1949) DNT	
T	*Rhodamnia blairiana* F.Muell.	Myrtaceae	–/– (2)	U	G		
T	*Rhodamnia spongiosa* (F.M.Bailey) Domin	Myrtaceae	–/– (2)	U	R		

T	*Rhodomyrtus pervagata* Guymer	Myrtaceae	–/– (3)	U	B2, G, R		
T	*Rhysotoechia mortoniana* (F.Muell.) Radlk.	Sapindaceae	–/– (1)	U	B2		
T	*Rhysotoechia robertsonii* (F.Muell.) Radlk.	Sapindaceae	–/– (1)	L	M		
V	*Ripogonum album* R.Br.	Smilacaceae	–/– (3)	U	B1, B2, G		
V	*Ripogonum elseyanum* F.Muell.	Smilacaceae	–/– (3)	U	B1		
V	*Rourea brachyandra* F.Muell.	Connaraceae	–/– (1)	L	M		
SH	*Rubus queenslandicus* A.R.Bean	Rosaceae	–/– (1)	U	B2		
T	*Ryparosa javanic*a (Blume) Kurz ex Koord. & Valeton[Δ]	Achariaceae[†]	+/+	L	M	Pammel (1911) *R. caesia* +CN; Rosenthaler (1919) *Ryparosa* spp. +CN	MELU102277
V	*Sarcopetalum harveyanum* F.Muell.	Menispermaceae	–/– (1)	B	B1	Webb (1949) DNT; Hurst (1942) –CN	
T	*Sarcopteryx martyana* (F.Muell.) Radlk.	Sapindaceae	DNT	U	G		
T	*Sarcopteryx reticulata* S.T.Reynolds	Sapindaceae	–/– (2)	L	M		
T	*Sarcotoechia lanceolata* (C.T.White) S.T.Reynolds	Sapindaceae	–/– (2)	U	G		
T	*Sarcotoechia protracta* Radlk.	Sapindaceae	–/– (3)	U	B1, G		
T	*Sarcotoechia* sp. (Mt Carbine *L.W.Jessup+ GJM995*)	Sapindaceae	–/– (2)	U	R		MELU102303
V	*Scaevola enantophylla* F.Muell.	Goodeniaceae	–/– (4)	U	B1, G	Webb (1949) DNT	
T	*Schistocarpaea johnsonii* F.Muell.	Rhamnaceae	–/– (5)	U	B1		
T	*Schizomeria whitei* Mattf.	Cunoniaceae	–/– (1)	U	G		
T	*Scolopia braunii* (Klotzsch) Sleumer	Salicaceae[†]	–/– (1)	U	B2		
T	*Siphonodon membranaceus* F.M.Bailey	Celastraceae	–/– (3)	U, L	B1, M		
T	*Sloanea australis* subsp. *parviflora* Coode	Elaeocarpaceae	–/– (4)	U	B1		
T	*Sloanea langii* F.Muell.	Elaeocarpaceae	–/– (5)	U, L	B2, G, M		
T	*Sloanea macbrydei* F.Muell.	Elaeocarpaceae	–/– (3)	U	B1, G		
V	*Smilax aculeatissima* Conran	Smilacaceae	–/– (3)	U	B1		
V	*Smilax calophylla* Wall. ex A.DC.	Smilacaceae	–/– (1)	L	M		
V	*Smilax glauca* Walter	Smilacaceae	–/– (2)	U	B1		
V	*Smilax glyciphylla* Sm.	Smilacaceae	–/– (2)	U	B2, R		
SH	*Solanum macoorai* F.M.Bailey	Solanaceae	–/– (1)	U	B2		
SH	*Solanum* sp.	Solanaceae	–/– (2)	U	B1		
SH	*Solanum viridifolium* Dunal	Solanaceae	–/– (1)	U	G		
T	*Sphenostemon lobosporus* (F.Muell.) L.S.Sm.	Sphenostemonaceae	–/– (3)	U	G, R		MELU102111
SH/T	*Steganthera australiana* C.T.White	Monimiaceae	–/– (2)	U	B2		
T	*Steganthera macooraia* (F.M.Bailey) P.K.Endress	Monimiaceae	–/– (4)	U	R		MELU102231
T	*Stenocarpus reticulatus* C.T.White	Proteaceae	–/– (1)	U	R	E. E. Conn (pers. comm.) –ve	MELU102196
T	*Stenocarpus sinuatus* (Loudon) Endl.	Proteaceae	–/– (1); flwr –	U	B2	E. E. Conn (pers. comm.) –ve	
V	*Stephania japonica* (Thunb.) Miers	Menispermaceae	DNT	L	M		
T	*Storckiella australiensis* J.H.Ross & B.Hyland	Caesalpiniaceae	–/– (3)	L	M		MELU102279
T	*Streblus glaber* var. *australianus* (C.T.White) Corner	Moraceae	–/– (3)	U	B2, R		
V	*Strychnos minor* Dennst.	Strychnaceae	–/– (1)	L	M		
T	*Symplocos cochinchinensis* subsp. 1	Symplocaceae	–/– (2)	U	G		
T	*Symplocos cochinchinensis* var. *gittonsii* Noot.	Symplocaceae	–/– (2)	U	B2, R		
T	*Symplocos cochinchinensis* var. *pilosiuscula* Noot.	Symplocaceae	–/– (3)	U	B2, G, R		MELU102218
SH	*Symplocos hayesii* C.T.White & W.D.Francis	Symplocaceae	–/– (3)	U	B1, B2, R		MELU102320
SH/T	*Symplocos paucistaminea* F.Muell. & F.M.Bailey	Symplocaceae	–/– (3)	U, L	B1, G, M		
T	*Synima cordierorum* (F.Muell.) Radlk.	Sapindaceae	–/– (1)	U, L	B2, G, M		
T	*Synima macrophylla* S.T.Reynolds	Sapindaceae	–/– (4)	U	B1, B2, G		MELU102289
T	*Synoum muelleri* C.DC.	Meliaceae	–/– (2)	U	B2		MELU102306
T	*Syzygium canicortex* B.Hyland	Myrtaceae	–/– (2)	U	B2, G		MELU102272

T	*Syzygium cormiflorum* (F.Muell.) B.Hyland	Myrtaceae	–/– (3)	U, L	B1, B2, G, M		MELU102224
T	*Syzygium endophloium* B.Hyland	Myrtaceae	–/– (4)	U	B1, B2, G, R		MELU102153
T	*Syzygium gustavioides* (F.M.Bailey) B.Hyland	Myrtaceae	–/– (1)	U	B1		
T	*Syzygium johnsonii* (F.Muell.) B.Hyland	Myrtaceae	–/– (3)	U	B2, G		
T	*Syzygium kuranda* (F.M.Bailey) B.Hyland	Myrtaceae	–/– (4)	U, L	B1, G, M		
T	*Syzygium luehmannii* (F.Muell.) L.A.S.Johnson	Myrtaceae	–/– (1)	U	R		
T	*Syzygium monospermum* Craven	Myrtaceae	–/– (1)	L	M		
T	*Syzygium papyraceum* B.Hyland	Myrtaceae	–/– (3)	U	B1, G		MELU102159
T	*Syzygium trachyphloium* (C.T.White) B.Hyland	Myrtaceae	–/– (1)	U	B1		
T	*Syzygium wesa* B.Hyland	Myrtaceae	–/– (3)	U	B2, G		MELU102096, 102249
T	*Syzygium wilsonii* subsp. *cryptophlebium* (F.Muell.) B.Hyland	Myrtaceae	–/– (3)	U	B1, G		MELU102223
SH	*Tabernaemontana pandacaqui* Lam.	Apocynaceae	–/– (1)	L	M		
SH	*Tapeinosperma* sp. (Cedar Bay *J.G.Tracey 14780*)	Myrsinaceae	–/– (4)	U	G		
SH	*Tasmannia insipida* R.Br. ex DC.	Winteraceae	–/– (3) dry*	U	R		
T	*Ternstroemia cherryi* (F.M.Bailey) Merr. ex J.F.Bailey & C.T.White	Theaceae	–/– (2)	L	M		
V	*Tetracera nordtiana* var. *nordtiana* F.Muell.	Dilleniaceae	–/– (2)	U, L	G, M		
T	*Tetrasynandra laxiflora* (Benth.) J.R.Perkins	Monimiaceae	–/– (6)	U, L	B1, G, M		MELU102229
T	*Timonius singularis* (F.Muell.) L.S.Sm.	Rubiaceae	–/– (1)	U	B1		
T	*Toechima erythrocarpum* (F.Muell.) Radlk.	Sapindaceae	–/– (3)	U, L	B1, G, M		MELU102321
T	*Toechima monticola* S.T.Reynolds	Sapindaceae	–/– (1)	U	G, R		MELU102098
T	*Triunia erythrocarpa* Foreman	Proteaceae	–/– (3)	U	B1	E. E. Conn (pers. comm.) –ve	
V	*Trophis scandens* (Lour.) Hook. & Arn. subsp. *scandens*	Moraceae	–/– (1)	L	M		MELU102271
V	*Uncaria lanosa* var. *appendiculata* (Benth.) Ridsdale	Rubiaceae	–/– (1)	L	M		
T	*Uromyrtus metrosideros* (F.M.Bailey) A.J.Scott	Myrtaceae	–/– (1)	U	R		MELU102315
V	*Ventilago ecorollata* F.Muell.	Rhamnaceae	DNT	L	M		
T	*Wilkiea angustifolia* (F.M.Bailey) J.R.Perkins	Monimiaceae	–/– (1)	U	B1		MELU102330
SH	*Wilkiea* sp.	Monimiaceae	–/– (2)	U	B1		
SH	*Wilkiea* sp. (Barong *L.W.Jessup 719*)	Monimiaceae	–/– (14)	U	B1, B2, G		
SH	*Wilkiea* sp. Gen. (AQ63687) sp. (Davies Creek *L.J.Webb+ 6430*)	Monimiaceae	–/– (3)	U	B1		MELU102302
SH	*Wilkiea wardellii* (F.Muell.) J.R.Perkins	Monimiaceae	–/– (3)	U	R		
T	*Xanthophyllum octandrum* (F.Muell.) Domin	Xanthophyllaceae	–/– (3)	U, L	B1, B2, G, M		MELU102101
T	*Xylopia maccreae* (F.Muell.) L.S.Sm.	Annonaceae	–/– (1)	L	M		
T	*Zanthoxylum veneficum* F.M.Bailey	Rutaceae	–/– (2)	U	B2, G	Webb (1949) DNT	MELU102215

† Species in the families Salicaceae and Achariaceae which, until recent revisions, were in the Flacourtiaceae (Chase *et al*., 2002)

‡ Non-woody *Alocasia brisbanensis* was not included in the analysis of the frequency of cyanogenic species.

Δ *Ryparosa javanica* is currently the subject of taxonomic review; this Queensland *Ryparosa* sp. is likely to be renamed (Webber, 2005).

* Due to limited access to foliage, tests for cyanogenesis using fresh tissue were not conducted, instead, freeze-dried samples were assayed quantitatively for the presence of CN indicated as 'dry'.