Fruiting Phenologies of Rainforest Plants in the Illawarra Region, New South Wales, 1988-1992

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Phenological patterns of fruit production have an important influence on the ecology of frugivores, and vice versa. A longitudinal study of fruiting cycles in rainforest plants was carried out in the Illawarra region between 1988 and 1992 as part of an investigation on food resources for frugivorous birds. A total of 82 species of fruit-producing plants were recorded, and seasonal availability of fruiting plants was examined by the mean number of species in crop production per month. Fruiting plants were available year round, with peaks occurring in autumn and early winter. The crop periods of most species were subject to substantial variability from year to year. There were no positive correlations between the monthly numbers of trees, and vines and climbers in fruit and climatic variables such as rainfall and temperature. Rainforests in southeastern Australia have lower botanical diversity than those of lower latitudes, attributing to substantial geographical variation in frugivore-plant relationships. Core crop periods were determined in 23 species of trees, three species of shrubs, six species of vines and climbers. Fruiting patterns in the remaining species were sporadic. Data presented in this paper provide baseline data for further studies, with important implications for natural resource and conservation management.

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KEYWORDS: ecology, fruit, Illawarra region, phenology, rainforest plants, seasonal patterns

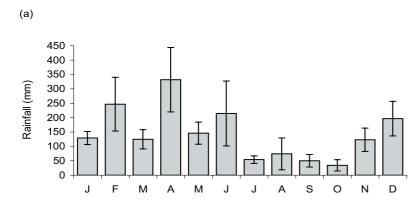
INTRODUCTION

Phenological patterns of fruit production in rainforest plants have an important influence on the ecology of frugivorous fauna. Typically, a large number of species exhibit irregular fruiting cycles (Frankie et al. 1974; Crome 1975; Foster 1982; Heideman 1989; Waterhouse 2001), forcing fruvigores to orientate their movements and dietary patterns in accordance to food availability. Seasonal abundance of fruit pigeons have correlated with fruiting phenologies (Crome 1975; Innis 1989). In tropical regions at least, the breeding seasons of some birds coincide with peaks in fruit abundance (Snow and Snow 1964; Crome 1975, 1976; Innis and McEvoy 1992). Other frugivores such as bowerbirds broaden their diet to include other plant and animal materials in order to remain sedentary during seasonal declines in fruit availability (Donaghey 1996; Frith and Frith 2004).

The relationship between frugivores and fruiting plants has value for the latter as well. In tropical

and subtropical regions, frugivores are considered 'keystone species' for their role in seed dispersal (Green 1993). For example, Webb and Tracey (1981) reported that fauna play a significant role in the reproductive cycles of more than 80 percent of flora in subtropical rainforests. In temperate climates, there is a shift toward rainforest flora relying more heavily on wind and hydrology as vehicles of seed dispersal, which is observed in a reduction in fruit-producing species (Blakers et al. 1984). Mills (1986) found that rainforests of the Illawarra region, south of Sydney, effectively lie in a transition zone between these two elements; a disproportionately high number of tree, shrub and climber species remained dependent on fauna, however herbs largely relied on abiotic strategies of seed dispersal.

Most of the rainforest areas of southeastern Australia have been severely depleted in size, which introduces an additional dimension of variability for frugivore-plant interactions. Ecological studies of rainforests at higher latitudes have important implications for natural resource and conservation



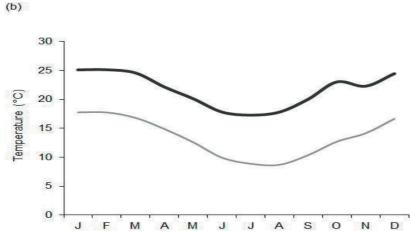


Figure 1. Climate statistics for the Wollongong University weather station between 1988 and 1992. Mean monthly rainfall (a) and mean maximum and minimum temperatures (b).

management. This paper reports on a five-year study of the fruiting phenologies of rainforest plants in the Illawarra region.

RAINFORESTS OF THE ILLAWARRA REGION

The Illawarra escarpment stretches approximately 50 km from the Royal National Park in the north to the Minnamurra Rainforest in the south (Macquarie 2013). This geographical area boasts a complex mosaic of different vegetation communities, including eucalypt forests, sparse woodlands and rainforests, especially on the higher altitudes (Ashcroft 2006). Rainforest sections to the east of the escarpment are supported by the slopes providing shelter from drying westerly winds, high rainfall generated by orographic precipitation (Bywater 1978; Reinfields and Nanson 2001, 2004; Macquarie 2013; Croke et al. 2014), perennial humidity (Fuller 1995; Ashcroft 2006) and low light penetration, especially in the cooler months (NSW NPWS 2011). The cliff line

forms the approximate watershed between two catchments (Switzer et al. 2005; Thornton et al. 2007), feeding the creeks that pass through rainforests and wet sclerophyll forests to the east (Mills 1998).

Many subtropical plants reach their southern limit in the Illawarra rainforests (Mills 1986). The unique vegetation communities in the Illawarra district have been attributed to the close proximity of the escarpment to the coast (Schulz and Magarey 2012), a warm temperate climate and fertile soils below the escarpment (French and Westoby 1992; NSW NPWS 2000). In general, subtropical rainforest occur on the lower slopes, and temperate rainforest on the upper slopes and gullies.

During the study period, the Illawarra region received a mean annual rainfall of 1726 mm (Australian Bureau of Meteorology, Wollongong University station, 1988-1992). Peaks in rainfall occurred in February, April and June, although the amount varied considerably from year to year (Fig. 1a).

Mean day temperatures ranged from 8°C (minimum; August) and 25°C (maximum; January) (Fig. 1b), similar to those reported by Ashcroft (2006).

METHODS

Study sites

The majority of this study was conducted at two sections of the Illawarra Escarpment State Conservation Area (Fig. 2). Mount Keira (34°24'S, 150°51'E, ~600ha area) was routinely surveyed via Robertson's Lookout, Byarong Park, the Mount Keira Ring Track (~5.5 km) and the Dave Walsh's Track (~800 m). The summit is 464 m above sea level. The foothills contain small isolated pockets of Illawarra Subtropical Rainforest, an endangered ecological community. Bulli Mountain (34°20'S, 150°54'E, ~100ha area) was routinely surveyed via Bulli Lookout and a walking track that extends to Sublime Point (~2.5 km). The plateau contains an isolated section

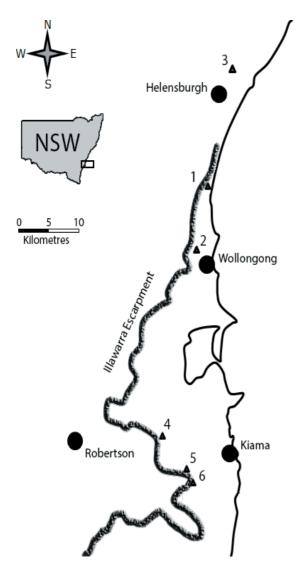


Figure 2. Locations of the main study sites, Bulli Mountain (1) and Mount Keira (2), and four additional sites, Bola Creek (3), Minnamurra Falls (4), Saddleback Mountain (5) and Foxground (6).

of Southern Sydney Sheltered Forest, an endangered ecological community that occurs on sandstone-shale transitional soils. Rare plant communities have been identified at both Bulli Mountain and Mount Keira (NSW NPWS 2011).

Occasional visits were also made to four additional sites containing remnant Illawarra rainforest: Bola Creek in the Royal National Park (34°9'S, 151°1'E, ~100ha area), Minnamurra Falls in Budderoo National Park (34°38'S, 150°43'E, ~90ha area), Foxground (34°43'S, 150°46'E, ~60ha area) and Saddleback Mountain (34°41'S, 150°47'E, ~70ha area) (Fig. 2). The former two were accessed via walking tracks maintained by the NSW National Parks and Wildlife Service. The rainforest remnant at

Foxground is mainly situated on private holdings and was surveyed by making observation while driving slowly along the road. Surveying of Saddleback Mountain was also carried out from a vehicle, with some sporadic explorations on foot, especially near the summit.

Data collection and analysis

The study design involved both routine surveys of the main sites (Mount Keira and Bulli Mountain) and sporadic surveying of the additional sites. The main sites were surveyed on a fortnightly basis between January 1988 and December 1992, hence providing a total of 132 field days. This involved traversing the established walking tracks and recording the presence of plants that produce fruits that could provide food resources for frugivorous birds, and whether fruiting was occurring. Additional trips to Bola Creek, Minnamurra Falls, Foxground and Saddleback Mountain broadened the area coverage of the study, and were undertaken monthly.

Plant species recorded were grouped into four broad categories: trees, shrubs, vines and climbers, and herbs. The fruiting periods for each species were determined at a monthly scale by pooling data from the five years of study. Core crop periods (CCP) for each species were determined based on fruit production occurring in the same months for at least three years.

The seasonal availability of fruiting plants was studied by examining the mean number of species in fruit per month. Linear regression analyses were applied to patterns in the number of fruiting species available (all plants, trees, and vines and climbers) and climatic variables (rainfall, maximum mean temperature, minimum mean temperature, and mean temperature). The limited numbers of shrub and herb species recorded were not sufficient for this analysis. Climatic data was sourced from the Australian Bureau of Meteorology (Wollongong University station). For trees, monthly means were also compared to the number of species fruiting reliably per month over the study period. In this context, reliability refers to fruit production occurring in a species in a month for three or more years.

RESULTS

This study recorded a total of 82 species of fruit-producing plants. Approximately half of these were trees (42 species). Shrubs, vines and climbers, and herbs comprised 15, 22 and three species respectively. The timing of fruiting in each species was generally simultaneous across all sites.

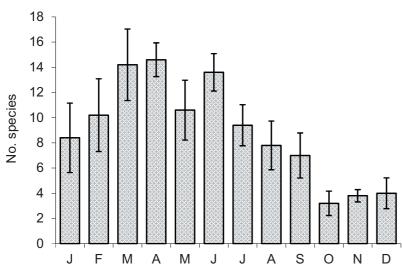


Figure 3. Mean number of fruiting species in the Illawarra rainforests between 1988 and 1992.

Seasonal patterns in fruiting periods

The fruiting periods of most species were extremely variable from year to year (Fig. 3). Overall, peaks in the mean number of species producing fruit occurred in autumn and early winter (March, 15.6 ± 2.8 ; April, 15.0 ± 1.3 ; June, 14 ± 1.5). The diversity of fruiting species available appeared to build up over the second half of summer (February, 11.2 ± 2.9) and decline over the winter months, reaching depression in spring (October, 3.2 ± 1.0 ; November, 3.8 ± 0.5).

Trees comprised approximately half of species recorded (42 species), and their seasonal pattern followed these trends (Fig. 4). The mean number of shrub species in fruit was greatest from mid summer to early autumn (January, 2.2 ± 0.7 ; February, 2.2 \pm 1.1; March, 3.0 \pm 0.8). In other times of the year, less than two species were fruiting in any one month. The mean number of vine and climber species in fruit was relatively consistent (~2.5 species per month), although troughs in fruiting species occurred in some of the warmer months (February, 1.2 ± 1.0 ; October, 0.4 ± 0.2 ; November, 0.4 ± 0.3 ; December, 0.6 ± 0.4).

Regression analyses did not detect any positive relationship between monthly availability of fruiting species (all plants, trees, and vines and climbers) and four climatic variables (rainfall, maximum mean temperature, minimum mean temperature and mean temperature) (Table 1). However, from a comparison between Figures 1 and 3, it appears that lowest overall fruit production occurs three months following the coolest and driest months.

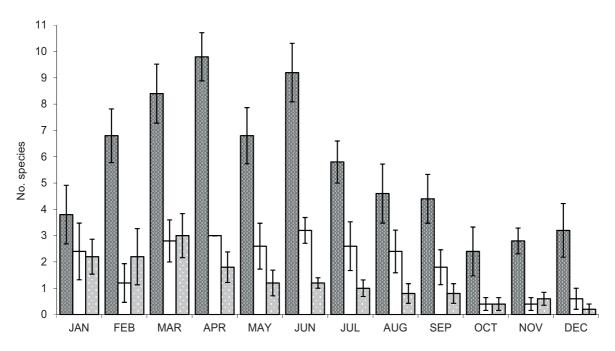


Figure 4. Mean number of fruiting species of trees (dark grey), vines and climbers (white) and shrubs (light grey) in the Illawarra rainforests between 1988 and 1992.

Table 1. R2 values resulted from regression analyses comparing the number of species in fruit with four climatic variables.

	\mathbb{R}^2	F _{1,59}	P								
ALL PLANTS											
Rainfall	0.05030	3.07186	0.00000								
Max Mean Temperature	0.00492	0.28650	0.02818								
Min Mean Temperature	0.00539	0.31452	0.01679								
Mean Temperature	0.00003	0.00168	0.03672								
TREES											
Rainfall	0.09163	5.85089	0.00000								
Max Mean Temperature	0.01172	0.68805	0.00812								
Min Mean Temperature	0.00028	0.01643	0.00216								
Mean Temperature	0.00188	0.10916	0.00794								
VINES AND CLIMBERS											
Rainfall	0.01176	0.69021	0.00000								
Max Mean Temperature	0.10492	6.79881	0.00028								
Min Mean Temperature	0.03289	1.97233	0.00083								
Mean Temperature	0.06428	3.98452	0.00074								

Fruiting periods of trees

Twenty-two species produced fruit on a reliable basis, that is fruiting occurred at a certain time of year for more than three years (50% of species recorded in the study) (Table 2). Monthly trends in the total number of species fruiting and the number of species fruiting reliably followed a similar pattern, except for reductions in the latter in May and December that did not correspond with the former (Fig. 5).

Of four species of figs recorded, only two had reliable fruiting periods. These were the Sandpaper Fig Ficus coronata and Moreton Bay Fig F. macrophylla, which both produced fruit reliably from summer to autumn. Koda Ehretia acuminata, Crabapple Schizomeria ovata and Brush Cherry Syzygium australe followed a similar seasonal pattern. Churnwood Citronella moorei mostly fruited in the latter half of summer. Yellow Ash Emmenosperma alphitonioides had a wide-ranging fruiting period, from late summer to early spring, but was only considered reliable in February and June.

The CCP of Jackwood Cryptocarya glaucescens, Sassafras Doryphora sassafras and Maiden's Blush Sloanea australis were apparently restricted to autumn. For species like Red Olive Plum Cassine australe, Sweet Pittosporum Pittosporum undulatum and Pencil Cedar Polyscias murrayi, reliable fruiting continued from autumn into winter. The CCP of Featherwood Polyosma cunninghamii continued until

early spring. Species like Lillypilly Syzygium smithii and Bolwarra Eupomatia laurina only fruited reliably in winter, and Yellow Pittosporum Pittosporum revolutum, Giant Stinging Tree Dendrocnide excelsa and Black Plum Diospyros australis were further restricted to early winter. In spite of this, some species with restricted CCP did sporadically produce fruit over a wider range, for example fruiting in Black Plum was observed from March to September.

Wild Quince Alectryon subcinereus and Cabbage Tree Palm Livistona australis also fruited reliably in winter, with their CCP extending to spring and early summer respectively. Fruiting in Brown Beech Pennantia cunninghamii was observed between September and February, but reliable fruiting was restricted to late spring and early summer.

Nine tree species only produced fruit in a single month throughout

the entire study period; three in autumn (Corkwood Endiandra sieberi, Deciduous Fig Ficus superba and White Beech Gmelina leichhardtii), one in winter (Illawarra Flame Tree Brachychiton acerifolius), two in spring (Red Ash Alphitonia excelsa and Murrogun Cryptocarya microneura) and three in summer (Native Carsacarilla Croton verreauxii, Flintwood Scolopia braunii and Whalebone Tree Streblus brunonianus). A further 11 species only fruited for a few months in one or two years.

Fruiting periods of shrubs

Fifteen species of fruit-producing shrubs were recorded in this study, three of which were invasive weeds (Table 3). Only 20 percent of species fruited reliably, while two species (Grey Myrtle *Backhousia myrtifolia* and Brittlewood *Claoxylon australe*) did not fruit during the study period. Orange Thorn *Citriobatus multiflorum* was the only native species that produced fruit reliably, with a CCP from winter to early spring. Indian Strawberry *Duchesnea indica* fruited sporadically in different months, but was only considered reliable in early autumn. The CCP of Jerusalem Cherry *Solanum pseudocapsicum* was from mid-summer to autumn, though some fruit also occurred in early spring.

Fruiting periods of vines and climbers

A total of 22 species of fruit-producing vines and

Table 2. Fruiting periods of tree species in the Illawarra rainforests. Numeric values represent the number of years fruiting occurred per month, and shading on values ≥ 3 years.

	J	F	M	A	M	J	J	A	S	0	N	D
White Aspen Acronychia oblongifolia									1	1	2	
Wild Quince Alectryon subcinereus				1		3	3	3	4	3	2	1
Red Ash Alphitonia excelsa										1		
Illawarra Flame Tree <i>Brachychiton acerifolius</i>								1				
Red Olive Plum Cassine australe		1	2	3	3	3						
Churnwood Citronella moorei	3	4	2			1						
Native Carsacarilla Croton verreauxii		1										
Jackwood Cryptocarya glaucescens			2	3	3	1						
Murrogun Cryptocarya microneura								1				
Giant Stinging Tree Dendrocnide excelsa					2	3		1				
Black Plum Diospyros australis			1	2	2	4	2	2	1			
Native Tamarind <i>Diploglottis australis</i>	2											1
Sassafras <i>Doryphora sassafras</i>			3	4	2							
Koda Ehretia acuminata	3	4	5	3	1							
White Quandong Elaeocarpus kirtonii	1	1										1
Yellow Ash Emmenosperma alphitonioides		3	2	2	2	3	2	1	2			
Corkwood Endiandra sieberi					1							
Bolwarra Eupomatia laurina				2	1	5	3	2	2			
Sandpaper Fig Ficus coronata	1	3	4	3								
Moreton Bay Fig Ficus macrophylla	3	4	3	1	1	1						2
Small-leaved Fig Ficus obliqua	2	1						1	2			
Deciduous Fig Ficus superba			1									
White Beech Gmelina leichhardtii			1									
Guioa Guioa semiglauca			2									
Native Mulberry Hedycarya angustifolia		1										1
Bolly Gum Litsea reticulata			1	1								
Cabbage Tree Palm <i>Livistona australis</i>	1					2	4	3	5	4	4	4
White Cedar Melia azedarach						2	1					
Brush Muttonwood Myrsine howittiana	1									1	2	1
Brown Beech Pennantia cunninghamii	1	1							1	1	4	4
Yellow Pittosporum Pittosporum revolutum				1	2	3						
Sweet Pittosporum Pittosporum undulatum			3	4	3	5	2	1				
Featherwood <i>Polyosma cunninghamii</i>			1	3	2	4	3	3	3			1
Pencil Cedar Polyscias murrayi				4	3	3	3					
Crabapple Schizomeria ovata		5	5	2	1							
Flintwood Scolopia braunii		1										
Maiden's Blush Sloanea australis				4	3	1	1	1				
Whalebone Tree Streblus brunonianus	1											
Brush Cherry Syzygium australe		3	4	4	1							
Lillypilly Syzygium smithii						2	4	3	1			
Red Cedar Toona ciliata		1	1	2	1							
Tree Heath Trochocarpa laurina							1			1		

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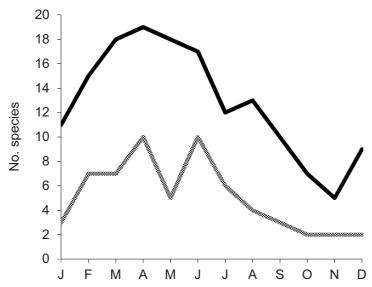


Figure 5. A comparison of monthly trends in the total number of tree species fruiting and the number of tree species fruiting reliably $(\geq 3 \text{ years})$.

climbers were recorded (Table 4), two of which were invasive weeds (White Moth Vine *Araujia sericifera* and Elmleaf Blackberry *Rubus ulmifolius*). Monthly

reliability was recorded in 27 percent of species. Wombat Berry Eustrephus latifolius had the most extensive fruiting period, covering 10 months of the year, though the CCP was between autumn and early spring. The CCP for Staff Vine Celastrus subspicatus, Water Vine Cissus hypoglauca and Jasmine Morinda Morinda jasminoides encompassed autumn and early winter, with each species producing fruit reliably in three months of the year. Native Grape Cissus antarctica was recorded fruiting from late autumn to spring, with a CCP between June and September. Pepper Vine Piper novaehollandiae produced fruit in the summer months, but was only reliable in January. There were five species recorded that were not observed fruiting at any time during the study period. These were Toothed Clematis Clematis aristata, Round-

leaf Vine *Legnephora moorei*, Milk Vine *Marsdenia rostrata*, Wonga-wonga Vine *Pandorea pandorana* and False Sarsaparilla *Smilax australis*.

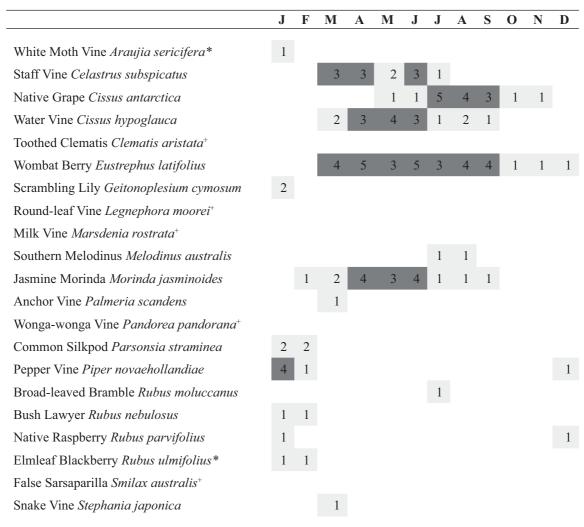
Table 3. Fruiting periods of shrub species of the Illawarra rainforests.

Numeric values represent the number of years fruiting occurred per month, and shading on values ≥3 years. *indicates an invasive weed species; +did not produce during study period

	J	F	M	A	M	J	J	A	S	O	N	D
Grey Myrtle Backhousia myrtifolia+												
Coffee Bush Breynia oblongifolia	2	1	2									
Orange Thorn Citriobatus multiflorum	1				1	3	3	3	3	2	2	
Brittlewood Claoxylon australe ⁺												
Prickly Currant Bush Coprosma quadrifida		1										
Indian Strawberry Duchesnea indica*	2	2	3		1						1	
Small-leaved Privett Ligustrum sinense*		1			1	1	1					
Cockspur Thorn Maclura cochinchinensis	1											
Mock Olive Notelaea longifolia	1											1
Bleeding Heart Omalanthus populifolius			1	1								
Hairy Psychotria Psychotria loniceroides			1									
Native Elderberry Sambucus australasica		1	2	2								
Native Grape Solanum aviculare	1	2	2	2								
Jerusalem Cherry Solanum pseudocapsicum*	3	3	4	4	3	2	1					
Common Wilkiea Wilkiea heugeliana								1	1			

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Table 4. Fruiting periods of vine and climber species of the Illawarra rainforests. Numeric values represent the number of years fruiting occurred per month, and shading on values ≥3 years. *indicates an invasive weed species; +did not produce during study period



Fruiting periods of herbs

Three species of fruit-producing herbs were recorded (Table 5). Settlers Flax *Gymnostachys anceps* exhibited a CCP from January to March, with fruiting also occurring through to June in 1992. Inkweed, an invasive weed, was only reliable in March, but also fruited until June in 1990. No CCP was determined for Black-fruit Saw-sedge *Gahnia melanocarpa*. This species only fruited in two months over the entire study period, which were February and March 1989.

DISCUSSION

The Illawarra region contains the most extensive area of rainforest in the Sydney Basin Bioregion (Erskine 1984; NSW NPWS 2002), but has not been

unaffected by extensive clearing (Mills 1998). The Illawarra rainforests are regionally significant as one of six major concentrations of rainforest in New South Wales (Floyd 1990), as well as the southern limit of the subtropical, warm temperate and littoral rainforest groups (Keith 2004; Schulz and Magarey 2012). This longitudinal study is unique in its focus on fruiting reliability, providing baseline information for further ecological study in the region, such as exploration of the carrying capacity of local frugivorous species.

In some tropical rainforests, strong correlations between peak fruiting periods and climatic factors, such as temperature and rainfall, have been demonstrated (Smythe 1970; Frankie et al. 1974; Humphrey and Bonaccorso 1979; Raemaekers et al. 1980; Foster 1982, 1985). In more temperate climates, this relationship is less evident (Yap 1982;

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Table 5. Fruiting periods of herb species of the Illawarra rainforests.

Numeric values represent the number of years fruiting occurred per month, and shading on values ≥3 years. *indicates an invasive weed species.

	J	F	M	A	M	J	J	A	S	O	N	D
Black-fruit Saw-sedge Gahnia melanocarpa		1	1									
Settlers Flax Gymnostachys anceps	3	4	3	1	2	1						
Inkweed Phytolacca octandra*			3	1	1	1						

Heideman 1989). The results of this study reflect the latter, in which the number of fruiting plants available did not directly correlate with seasonal variations in rainfall and temperature. Peaks in the mean monthly availability of fruiting plants occurred in autumn and early winter, apparently following on from warmest and wettest parts of the year by periods of lag of up to three months. Fruiting plants were available in all months despite obvious fluctuations in seasonal diversity.

The number of fruit-producing plants is dramatically reduced in the Illawarra rainforests compared with the species assemblages observed in tropical regions (Blakers et al. 1984). This raises the need to understand fruiting phenologies in view of the ecology of frugivores (Waterhouse 2001). The Illawarra rainforests are a significant area for frugivores listed under the NSW Threatened Species Conservation Act, such as the Grey-headed Flying Fox Pteropus poliocephalus (Parker et al. 2008), as well as three species of fruit doves *Ptilinopus* sp. that have been recorded as vagrants (Wood and Simcock 1993; Schulz and Ransom 2010). The region has also been identified as core habitat for such species as the Green Catbird Ailuroedus crassirostris (NSW NPWS 2011; Schulz and Magarey 2012).

Many of the major food items of fruit pigeons recorded in southeastern Queensland (Innis 1989) were not available in the Illawarra region. Consequently, the diet of Topknot Pigeons Lopholaimus antarcticus in the Illawarra rainforests differed from other parts of their distribution (Crome 1975; Innis 1989), with a focus toward fruiting plants that produced at least one good crop season in five years (Waterhouse 2001). Similarly, at least two-thirds of the diet of the Green Catbird Ailuroedus crassirostris, a regionally important species, comprised of species that produced fruit with reliable seasonality (Mo and Waterhouse, unpub. data; cf. Innis and McEvoy 1992). The identification of important feed species and knowledge of its phenology provides a more informative basis for rainforest restoration, which is currently underway in many private landholdings.

Anthropogenic factors present further implications for the ecology of fruiting plants and frugivores. Like many of the rainforest areas of southeastern Australia, the Illawarra region has experienced extensive clearing of natural vegetation. European settlement began around 1815, during which time the rainforests were believed to cover a total area of at least 22 850 ha (Mills 1986). The plentiful supply of Red Cedar Toona ciliata attracted private timber getters, which in turn opened up the region for pastoral and agricultural land uses (MacDonald 1966; Hunter 1974; Bywater 1978; Dunstan and Fox 1996; Adams 2005). In areas of mild topography, the fertile soils were exploited for growing crops (Mitchell 1997). Today, less than 6000 ha of rainforest remain, a mere quarter of its original area (Mills 1986; Stork et al. 2008; Riviere and Rowlatt 2013; Mo and Waterhouse 2015). Its dramatic reduction has heightened the need for thorough studies (e.g. Bywater 1978; Floyd 1982; Erskine 1984; Mills 1998), in particular those focusing on biodiversity and geographical significance.

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