Phenology, seasonality and trait relationships in

a New Zealand forest

SHARADA PAUDEL

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SUPERVISORS

Associate Professor Kevin Burns (Primary Supervisor) Victoria University of Wellington

Associate Professor Ben Bell (Secondary Supervisor) Victoria University of Wellington

Abstract

The phenologies of flowers, fruits and leaves can have profound implications for plant community structure and function. Despite this only a few studies have documented fruit and flower phenologies in New Zealand while there are even fewer studies on leaf production and abscission phenologies. To address this limitation, I measured phenological patterns in leaves, flowers and fruits in 12 common forest plant species in New Zealand over two years. All three phenologies showed significant and consistent seasonality with an increase in growth and reproduction around the onset of favourable climatic conditions; flowering peaked in early spring, leaf production peaked in mid-spring and fruit production peaked in mid-summer coincident with annual peaks in temperature and photoperiodicity. Leaf abscission, however, occurred in late autumn, coincident with the onset of less productive environmental conditions. I also investigated differences in leaf longevities and assessed how seasonal cycles in the timing of leaf production and leaf abscission times might interact with leaf mass per area (LMA) in determining leaf longevity. Leaf longevity was strongly associated with LMA but also with seasonal variation in climate. All 12 species produced leaves in spring and abscised leaves in autumn. Nevertheless, leaf longevity ranged from 6 months to 30 months among species, leading to several distinct leaf longevity categories (i.e. 6-7 months, 15-18 months and 27-30 months). Finally, I examined the relationship of leaf traits with flower and fruit traits and their relation to the global leaf economic spectrum (LES) that describes multivariate correlations between a combinations of key leaf traits. The results resonated with the patterns of leaf economic spectrum for New Zealand species and provided evidence for significant correlations between leaf and fruit traits,

indicating that plants with long lived leaves and higher LMA produce fruits that take more time to develop, stay on the plant longer and have larger seed size. This study contributed to bridging the gap in our understanding of the relationship between vegetative and reproductive traits, it has increased our understanding of phenological patterns in New Zealand forests, and when viewed with earlier phenological studies, provides a first step towards understanding how New Zealand forest might respond to global climate change. In addition, the research illustrates how seasonality in climate can constrain the life times of leaves. In the context of global trait research culminating into the whole plant economics spectrum, this study provides clear evidence of leaf and fruit phenological and morphological trait associations. It helps to further our understanding of phenology, seasonality and plant trait relationships for some common tree species in New Zealand and presents some novel findings that provide a basis for future research.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Phenology

Phenology, the science of appearance, originated from the Greek, *phainein,* meaning to show or appear (Lieth, 1974; Schnelle, 1955). It is used to study timing of recurring life cycle events, for example leaf unfolding, leaf abscission, flowering in plants, or migration times in birds and hibernation in some animals (Fenner, 1998; Dubé et al., 1984). Phenological events have served as a natural calendar of unfolding events since pre-agricultural times (Schwartz, 2003; Chu, 1973, 1931). Keeping the records of interesting phenological events once started as pleasure and curiosity by keen naturalists, now is a useful branch of science (Greene, 1983). Phenology today has a wide range of applications in agriculture, forest management, allergy management and biological events management, among others (Denny et al., 2014; Morisette et al., 2009; Haggerty & Mazer, 2008; Beggs, 2004; Wallace & Painter, 2002). Most of all, the records of timing of phenological events over the last decades have gathered attention as bioindicators of climatic patterns in response to globally rising temperatures (Rosenzweig et al., 2007; Menzel et al., 2006; Badeck et al., 2004; Walther et al., 2002; Schnelle, 1995).

Phenology can be studied from the individual to the community level, or at the individual or species scale, or at a particular phenological event such as leafing, flowering or fruiting in plants, or at developmental stages of an individual leaf, flower or fruit (Primack, 1985). These distinct but interdependent phenological events in plants such as bud-burst, leaf-expansion, abscission, flowering, fertilisation, seed-set, fruiting, seed dispersal and germination all recur at synchronised intervals (Fenner, 1998). The events and synchronicity might have been shaped by several biotic and abiotic factors together

with ecosystem processes as such as competition, resource partition and allocation (Badeck et al., 2004; Rathcke & Lacey, 1985; Leith, 1974).

Phenology has widely been used to monitor adaptive traits of plants and evaluate these relationships within ecosystems, in addition to its widespread applied usage to monitor crop production and the evaluation of primary productivity (Arora & Boer, 2005; Sakamoto et al., 2005; Goetz & Prince, 1996; Rathcke & Lacey, 1985). Additionally, in recent times phenology has been prominently utilised in climate change research (Cleland et al., 2007; Visser & Both, 2005; Edwards & Richardson, 2004; Walther et al., 2002). A global rise in temperature could have major consequences for ecology. The responses of the changing climate are visible in the physiology and phenology of organisms, the distribution of species and their interactions, and the composition and structure of communities (Visser & Both, 2005; Dunn, 2004; Parmesan & Yohe, 2003; Root el al., 2003; Walther et al., 2002; Hughes, 2000). Current understanding and usage of phenology would assist scientists in managing and mitigating the effects of climate change through planning and resource management (Denny et al., 2014; Morisette et al., 2009).

Each phenological event has a part to play in the progression of plant growth, reproduction and survival. Optimal timing for flowering and fruiting are essential for successful pollination and subsequent seed dispersal (Primack, 1987). Apart from the availability of pollinators and dispersers, flowering and fruiting also depend on the suitability of climatic variables such as moisture availability and photoperiodicity and the modes of pollination and dispersal such as by the wind or by birds (Elzinga et al., 2007;

Newstrom, Frankie, & Baker, 1994; Rathcke & Lacey, 1985). Leaf phenology, however, serves three different purposes in the plant's life. Leaf production guarantees optimal primary productivity, leaf abscission ensures energy conservation and leaf longevity relates to the photosynthetic return of a plant's investment on leaves (Kikuzawa & Lechowicz, 2011; Wright et al., 2004; Noma & Yumoto, 1997; Kikuzawa, 1983). The timing of leaf production and leaf abscission determines the length of the growing season which drives the carbon acquisition in terrestrial ecosystems (Cleland et al., 2007). Usually leaf phenology is linked to climatic variables such as temperature, rainfall, irradiance or photoperiod (Fenner, 1998; Wright & van Schaik, 1994; Lieth, 1974). In temperate regions, the favourable climatic conditions such as increasing temperature and longer sunshine hours brought by spring are often linked to bud break and leaf emergence patterns, which heighten plant productivity, while increasing rainfall intensity, decreasing temperature and frosts in winter may trigger leaf loss (Kikuzawa, 1990).

Plants are exposed to seasonal fluctuations of climate and resources. Seasonality brings either regular or periodic changes to a wide range of proximate environmental factors such as temperature, precipitation, humidity, wind speed, insolation and day length, or to ultimate factors such as pollinators and dispersers. All these factors contribute to shaping the phenological behaviour and timing of plant species and communities (Menzel, 2003). Seasonality in resources in turn results in seasonality in phenology such as leaf producing seasons, leaf abscission seasons, flowering seasons and fruiting seasons. Though there are year to year variations in timing or calendar dates of these phenological events, some seasonal events are reliably accurate such as the return of

migratory birds and coinciding it with pollination and seed dispersal (Newton, 2008). Seasonal climates in temperate regions result from high annual variation in environmental conditions which reciprocate to the seasonal plant phenology, but nevertheless tropical regions also display fluctuations in environmental conditions along with phenological patterns, although the amplitude of variations differ (Kramer et al., 2000, Van Schaik et al., 1993).

1.2 New Zealand forest phenology

New Zealand forests lost considerable coverage since the arrival of humans 700 years ago and subsequent introduction of mammalian herbivores and predators (Holdaway, 1989; King, 1984). Initially forests were cleared for agriculture and settlement, subsequently exotic mammalian herbivores and predators were introduced, which eventually had a substantial effect on New Zealand avifauna. Approximately, 29% of native birds went globally extinct and 45% of them were eliminated from the mainland New Zealand, particularly prompted by mammalian predators such as rodents (*Rattus exulans, R. norvegicus, Mus musculus & R. rattus*), stoats (*Mustela erminea*) and feral cats (Atkinson & Cameron, 1993; Diamond & Veitch, 1981). The Australian brushtail possum introduced in New Zealand in the latter half of 19th century rapidly spread throughout the country and heavily browsed the native forests, and is also known to feed on fledging birds and invertebrates (Trewick & Morgan-Richards, 2014; King, 2005; Wilson, 2004; Fitzgerald & Wardle, 1979; Fitzgerald, 1976; Gilmore, 1967; Gilmore, 1965). This instigated several studies on the effects possums on New Zealand forests

and agricultural as well as pastoral land (Harvie, 1973; Gilmore, 1965; Kean & Pracy, 1953). Phenological and forest ecology studies were also carried out to understand the fluctuations of intensity and duration of food availability identified in possums' faecal analysis (Fitzgerald, 1976; Mason, 1958). The role of other predators such as mustelids and rodents were reviewed later by O'Donnell (1996) in the context of declining New Zealand bird populations.

An elaborate and intensive study on the forest community in the Orongorongo Valley was conducted from 1966 to 1990 which included a two year phenological study of five plant species identified as plants preferred by possums (Brockie, 1992; Fitzgerald, 1976). Wardle (1984) discussed the reproduction and tree growth phenology of New Zealand beech forests and suggested that beeches were an alternative food choice for possums. To investigate the impacts of large scale logging on a bird community in South Westland, O'Donnell and Dilks (1994) studied bird population distribution, their food and foraging patterns between 1983 and 1985. This study also included flowering and fruiting phenology of over 40 plant species to describe seasonal variation in the use of food sources.

Phenology is widely used in understanding terrestrial and community ecology and ecosystem processes. Between 1962 and 1964 Wardle observed leaf production, leaf fall, cambial activity and growth rates of five native and one introduced species in South Island locations (Wardle, 1968a). The results of this study were discussed further by Wardle (1978) who also reviewed flowering and fruiting studies available at the time. Wardle (1978) recommended successive annual phenological observations to better understand the phenology of New Zealand plants. Primack (1980) conducted a detailed

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study of variation in flowering phenology of three species for two growing seasons in the Upper Waimakariri River Basin, South Island. Flowering times were compared between species and between sites and also checked for correlation between variation in flowering times and the number of flowers and fruits per plant. Multiple year phenological observations are also beneficial for identifying and predicting future masting events. Studies on masting behaviour and consequences are mostly species specific, such as in some species of *Nothofagus* (beeches), *Dacrydium* (rimu), *Phormium* (flaxes) and *Chionochloa* (tussocks) (Fitzgerald, Efford & Karl 2004; Kelly & Sork, 2002; Schauber et al., 2002; McKone, Kelly & Lee, 1998; Kelly, 1994; Robert & Platt, 1990; Norton & Kelly, 1988).

Fruit and flower phenologies have implications on reproductive success of an individual through pollination and seed dispersal (Howe & Smallwood, 1982). Fruit and seed properties of 56 woody plant species in Ahuriri Summit Bush Reserve and 36 species in Banks Peninsula along with relationships between fruits and frugivores were discussed in the context of avian seed dispersal by Burrows (1994a, 1994b). Phenological observations as a part of this study aimed to gather information on fruit types, degree of fleshiness, fruit sizes, and seed numbers, and hence to speculate on the evolution of the mutualistic relationship between fleshy fruited flora and frugivores. New Zealand has a high proportion fleshy fruited flora (72% of trees), 250 species from 50 families (Burrows, 1994; Clout, Karl, & Gaze, 1991). Even though a small percentage of genera (4%) are prominently bird-pollinated, apart from one nectivorous bat species (Arkins et al., 1999), and some reptiles (Whitaker, 1987), birds are likely to fill the roles of both pollinators and dispersers (Anderson et al., 2006). Flowering and fruiting phenology is

widely used to explore seasonal variation in fleshly fruit availability to birds and the possible consequences.

Williams and Karl (1996) explored fruiting phenology of native and introduced plant species and seasonality of diets of birds in the Nelson area and compared the diets of endemic, non-endemic and adventive bird species in there. Perrott and Armstrong (2000) evaluated the availability of fruit and flower food sources to the reintroduced hihi (stitchbird, *Notiomystis cincta*) population in Mokoia Island, North Island. They collected information on vegetation composition, density, distribution and phenology of plant species likely to be preferred by hihi. To address the lack of pollination studies in New Zealand plants, Lloyd (1985) reviewed the floral biology, flower characteristics and peculiarities of New Zealand flowers and discussed plant-pollinator relationships. Newstrom & Robertson (2005) reviewed the overall progress in our understanding of pollination systems in New Zealand. Despite New Zealand being characterised as a low pollinator dependent flora, primarily due to its isolated nature, they found angiosperms there possessed sexual features that indicate dependence on pollen vectors.

The New Zealand flora is highly evergreen, only 27 species (5% of the species) have significant leaf loss in winter and only 10 species are fully deciduous (Atkinson & Cameron, 1993). There are fewer multispecies and multiyear phenological studies of leaf phenology in New Zealand compared to flower and fruit phenology studies in New Zealand. New growth phenology was documented to quantify the browsing effect of the brushtail possum in 1970s and 1980s (Fitzgerald, 1976; Meads, 1976), as noted earlier, or for assessing the feeding pattern of, and food availability to, native bird species (Leathwick, 1981; O'Donnell & Dilks, 1994). Leaf production and abscission phenological

studies, however, are sparsely concentrated on a few species such as *Hoheria glabrata* (Haase, 1987), *Aristotelia serrata* and *Fuchsia excorticata* (Dungan et al., 2004; Dungan et al., 2003a). McGlone et al. (2004) reviewed deciduousness in the New Zealand native flora, specifically the patterns of winter leaf loss, and explored the possible reasons for the small percentage of flora displaying deciduousness in New Zealand. With no extensive domination of deciduous species, New Zealand forests are green throughout the year (McGlone et al., 2004). These features contrast with the temperate zone of the Northern Hemisphere where deciduous species are widespread and have total leaf loss with the arrival of winter (Kikuzawa, 1983).

The majority of studies on plant phenology are focused on either reproductive strategies of plants, or the importance of flowers and fruits as food for their pollinators or dispersers, or the pests of native flora and fauna (Cummings et al., 2014; Dijkgraaf, 2002; Perrott & Armstrong, 2000; O'Donnell & Dilks, 1994; Fitzgerald, 1976). There is earlier documentation of seasonality in New Zealand plants in different locations and topographies (Primack, 1980; Wardle, 1978; Clarke, 1968; Scott, 1960). However, some are based on limited observations (Wardle, 1978) and some lack successive annual observations of individual plants. Similarly, leaf phenology has received relatively less attention in the literature and has been mostly limited to deciduous species. In addition, though individual phenological stages such as flowering or fruiting have been the focus of some studies, there is a gap in studies dealing jointly with reproductive and vegetative phenologies at the community level in recent times. The community level patterns of flowering, fruiting and leafing phenologies extend our knowledge on seasonality in New

Zealand forests, with additional possible benefits to conservation planning and to climate change research.

1.3 Worldwide leaf economic spectrum

Despite large variation in leaf morphology amongst over 250,000 plant species around the world, a distinctly limited set of leaf traits and combinations have given rise to a framework of plants called the "leaf economic spectrum" to explain the tradeoff between growth, survival and reproduction (Diaz et al., 2016; Wright et al., 2004). The spectrum runs crudely from short-lived, highly metabolizing leaves with quick return of investment to long-lived tougher leaves with slow return of investment (Santiago, 2007; Wright et al., 2004). The central axis of the spectrum explains the strategy of plants to efficiently deploy available resources in order to maximize carbon gain (Whitfield 2006). The worldwide leaf economics spectrum is widely cited and further investigated by scientists from various disciplines and is seen as one of the most influential explanations for leaf trait variation (Donovan et al., 2011).

Six key leaf traits (leaf mass per unit area, leaf lifespan, leaf nitrogen and phosphorus content and rates of photosynthesis and respiration) from more than 2000 species around the world were compiled and analysed for trait associations. The central axis of the spectrum captured 74% of variation in the six key traits. The multivariate correlations explained by the spectrum and its alignment on one central axis suggested that the other plant traits and plant processes are also related to the leaf economic spectrum (Burns & Lake, 2009; Santiago, 2007; Poorter & Bongers, 2006). The spectrum

has been subsequently tested for more species from more locations and also for more leaf traits as well as other plant traits such as plant height, wood density, and the morphology and physiology of stems and roots (Blonder et al., 2011; Chave et al., 2009; Laughlin et al., 2010; Niinemets et al., 2007). Recent studies have given emphasis to whole plant trait correlations as the focus for future global trait research (Díaz et al., 2015).

Central leaf economic traits

SLOW { Photosynthetic rate (nmol g^{-1} s^{-1}) → Respiration rate (nmol g^{-1} s^{-1}) → } FAST

LESS NUTRITIOUS { Leaf nitrogen (%) → Leaf phosphorus (%) → } MORE NUTRITIOUS

LONG ← Leaf lifespan (months) SHORT

THICK, DENSE ← Leaf mass per area (g m^{-2}) THIN, LESS DENSE
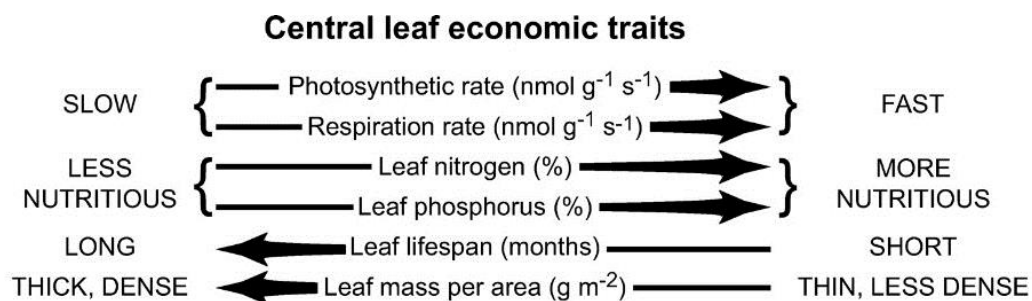
Figure 1.1: Leaf trait variation in the leaf economic spectrum. The leaves with the characteristics on the left have high leaf mass per unit area (LMA) and relatively greater longevity compared to leaves on the right. The thickness of arrows increases with higher values of particular traits.

The metabolism of plants is determined by their photosynthetic rates. Plants with high photosynthetic rates and with high metabolism acquire resources at a faster pace, hence plants with fast turnover times in leaf carbon may have faster reproductive turnover times too (Reich, 2014; Burns & Lake, 2009; Santiago, 2007). Integration of phenological research into trait research combines time and traits together which could complement

and contribute to global trait research. Additionally, the relationship between investment in leaves, flowers and fruits would elaborate our understanding of the whole plant perspective. Based on the concept of the leaf economics spectrum, this study tested the concept for some common indigenous plant species in New Zealand and evaluated whether plants with more active leaves with higher photosynthetic rates and shorter lifespan would have a shorter reproductive phenology, whereas plants with higher leaf mass area, lower photosynthetic rate and longer lived leaves might have a longer reproductive phenology. I examined leaf traits, leafing phenology and reproductive phenology of plants to establish these relationships amongst them. Also, since none of the species in this study were included in the original dataset of the worldwide leaf economics spectrum, it was relevant to test the theory of the leaf economics spectrum for new species.

1.4 Thesis Structure

The main focus of my thesis was to identify seasonality in phenologies in a New Zealand forest and to determine whether seasonality in some phenologies are constrained by seasonality in climate and to identify relationships between plant life-history traits and the leaf economic spectrum.

Chapter 2 gives a brief introduction to the study area, study species and general phenological methods used to acquire data for this thesis.

Chapter 3 is based on two years of phenological observations on leaf, flower and fruit phenologies where I tested for seasonality in each phenological event, determined the mean peak timings of these phenological events for each species as well as for each phenological event and finally discussed the climatic conditions at the peak of each phenological event.

Chapter 4 aimed at exploring seasonality in phenology and to further understand vegetative phenologies and their relationships to the global trends portrayed in leaf traits. The phenological observations from Chapter 3 were complemented by leaf longevity and leaf mass per unit area (LMA) measurements for each species to explore their relationship and differences between species and the influence of seasonality of climate on their leaf phenology. The leaf economic spectrum was confirmed to operate consistently for a number plants traits other than the leaf traits, however inclusion of reproductive traits gives greater understanding and validation in terms of the interpretation of whole plant trait correlations.

In Chapter 5, I confirmed that leaf traits of New Zealand plant species are correlated with each other in a similar manner postulated by the leaf economic spectrum. I also tested whether phenological and morphological traits governing flowers and fruits are also related to leaf traits.

Finally in chapter 6, I present a summary of the thesis, some important implications, future directions and conclusions. The three data chapters (3-5) are intentionally written as independent manuscripts, so there is inevitable repetition of some of their contents.

CHAPTER 2

STUDY AREA, STUDY SPECIES AND PHENOLOGICAL METHODS

2.1 Study area

The study was conducted in ZEALANDIA, a forested sanctuary, located in the foothills above Wellington, on the southern tip of the North Island of New Zealand (41° 18.3´S, 174° 44.8´E). ZEALANDIA, formerly known as Karori Wildlife Sanctuary, is a part of remnant forest in Kaiwhawhara Valley within Wellington City. It encompasses 225 hectares of coastal broadleaf forest that was burnt and cleared in the late nineteenth century for agriculture and farming. Originally, the area was covered with podocarp/broadleaf rainforest with emerging *Dacrydium cupressimum* (rimu), *Prumnopitys ferrugninea* (miro) and *Metrosideros robusta* (northern rata), over a canopy of *Beilschmeidia tawa* (tawa) and *Alectryon excelsus* (titoki) (Burch, 1997). Later, from the 1870's to 1992, the sanctuary area was closed to public access and dams were built to create two water supply reservoirs for Wellington City Council (Mahat, 2000). In 1992, Forest and Bird (a non-government organisation working in the conservation sector in New Zealand) recommended that the area be a "high priority site with extremely high natural values and restoration potential" which needed "protection and conservation" (Campbell-Hunt, 2002).

ZEALANDIA now supports a diverse regenerating native forest dominated by *Melicytus ramiflorus* (mahoe), *Pseudopanax arboreus* (five finger), *Beilschmeidia tawa* (tawa), *Dysoxylum spectabile* (kohekohe), *Elaeocarpus dentatus* (hinau), *Knightia excelsa* (rewarewa) and remnant exotic pine species (e.g. *Pinus radiata*) with an understorey of vines, shrubs and tree ferns. A pest eradication programme and specially-designed fence to exclude invasive mammals have enhanced the regeneration of vegetation and return

of native birds, supplemented with reintroductions (Bell, 2015; Burns, 2012; Karori Wildlife Santuary Trust, 1997; Fuller & Lynch, 1994).

The sanctuary lies 160m to 356m above sea level. The slopes of the study sites ranged from 18° to 30°. The climate is mild and temperate with an average range of daily temperature between 6°C and 21°C annually (NIWA, 2014). Annual rainfall totals 127 cm and there is an average of 2000 hours of sunshine annually. The area experiences significant wind gusts, greater than 60 km/hr for an average of 173 days per year. Summers are warm and breezy, while winters are mild with occasional southerly winds and frosts. Temperature and sunshine hours gradually increase with the onset of spring, peaking in summer, while rainfall decreases through spring and summer and peaks in winter.

Actual evapotranspiration, which serves as a proxy for primary productivity, is an amalgamation of temperature, precipitation and solar radiance (Ting, Hartley, & Burns, 2008). Thus, to evaluate the climatic drivers of each phenological stage, mean monthly values of temperature, rainfall and sunshine were obtained online from a database of NIWA (National Institute of Water and Atmospheric Research) (Chappell, 2014). Patterns in plant phenologies were then compared to climatic variables graphically to identify the climatic conditions coincident with each phenological stage.
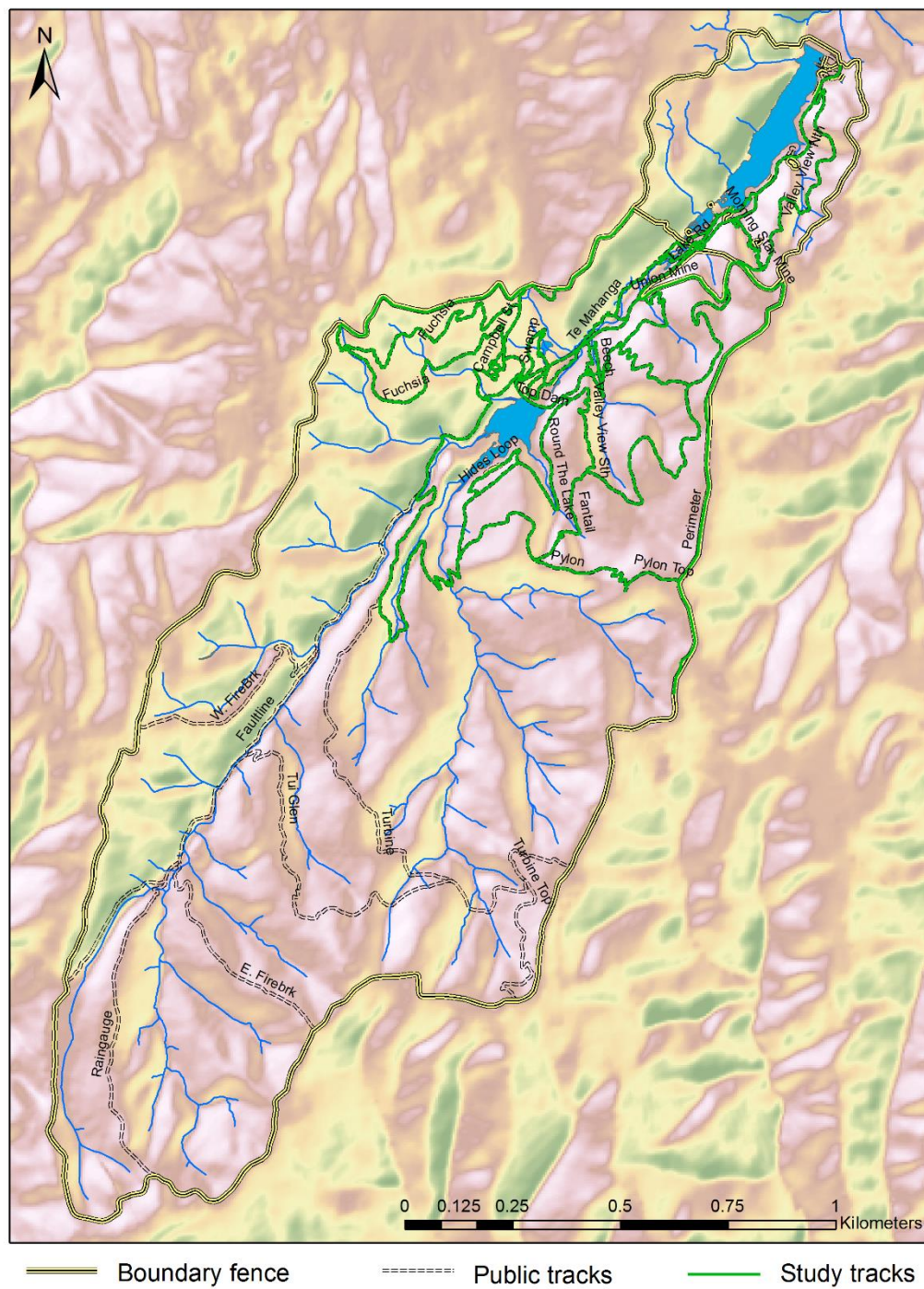
Figure 2.1 A map of ZEALANDIA with established tracks used for phenological sampling

(Source: ZEALANDIA Shapefiles).

2.2 Study species

This section provides a brief introduction on the plant species studied. There is a brief overview of national distribution, growth form, some morphological traits, pollination type and dispersal modes for each species. Nomenclature for the plants follows Dawson & Lucas (2000), with species descriptions acquired mainly from Dawson and Lucas (2000), Allan (1961), http://nzpcn.org.nz, http://terrain.net.nz or any other relevant literature as cited in the species descriptions that follow.

Aristotelia serrata

Aristotelia serrata (common name Wineberry, family Elaeocarpaceae), is found throughout New Zealand in moist lowland and mountain forests and damp river ridges. It grows up to 10m tall with up to 30cm trunk diameter. Wineberry is dioecious with separate male and female plants, leaves are serrated, broad and thin, 5-12cm long and 4-8cm wide, flowers are rose coloured small and numerous about 4mm wide and fruits are berries, dark red to black and about 5mm wide. Wineberry flowers are bird pollinated and the seeds are bird dispersed. In ZEALANDIA, they are distributed mostly along the Valley View Track surrounding and overlooking the lower lake facing north-west.

Fuchsia excorticata

Fuchisa excorticata (common name Tree Fuchsia, family Onagraceae) is a native deciduous tree found commonly in moist lowland to mid-mountain forests throughout New Zealand, more prominent in regenerating forests and alongside creeks and rivers.

It grows up to 12m tall with trunk 60cm in diameter and bears thin leaves 3-10cm long and 1.5-3cm wide. The flowers are green when young and change to red 2-3cm long and nectar rich when mature. These flowers are popular among native honey-eating birds such as tui, bellbirds and silvereyes. The fruits are dark purple berries about 1cm long, also dispersed by frugivory. In ZEALANDIA, tree fuchsia is distributed mostly around riverbanks of the lower lake along Te Mahanga track, Jim and Eve Lynch track and the Fuchsia track.

Geniostoma rupestre (G. ligustrifolium var ligustrifolium)

Geniostoma rupestre (common name Hangehange, family Loganiaceae) is a native understorey shrub found in lowland and coastal forests throughout the North Island and northern part of the South Island. It can grow up to 3m tall, bears pale green opposite leaves 5-7cm long and 2-3cm wide, flowers are small, green animal pollinated and fruits are dry capsules dispersed through frugivory. In ZEALANDIA, Hangehange trees are mostly distributed along the Round the Lake track on north facing slopes of the upper lake area.

Pittosporum eugenioides

Pittosporum eugenioides (common name Lemonwood, family Pittosporaceae) is a native tree found in coastal to lower mountain forests throughout New Zealand. It grows up to 12m tall and up to 60cm diameter trunk. The leaves are yellow-green 5-10cm long and 2.5-4cm wide, with undulated margins and when crushed have a smell of lemon. The flowers are small yellow 1.5cm in diameter growing in terminal clusters, pollinated by

birds and insects and fruits are capsules 5-6cm long with black sticky seeds that are animal dispersed. In ZEALANDIA, lemonwood trees were studied along the Valley View track and Round the Lake track, however they are also found elsewhere within the sanctuary.

Coprosma grandifolia

Coprosma grandifolia (common name Kanono, family Rubiaceae) is a native shrub or small tree found in moist sheltered lowland and the mid-montane forests all over New Zealand. It can grow up to 6m and leaves are 15-20cm long and 7-10cm wide. *Coprosma grandifolia* is dioecious, flowers have dangling toothed glands and is wind-pollinated and fruits are orange berries, 7-9mm, bird-dispersed. Kanono trees are found all over ZEALANDIA, mostly studied along the Lake Track, Swamp Track, Round the Lake Track and Valley View Track.

Coprosma robusta

Coprosma robusta (common name Karamu, family Rubiaceae) is a native shrub or small tree found in lowland forests throughout North Island. It can grow up to 6m and leaves are smaller than other Coprosmas, 5-13cm and 3-4cm wide. *Coprosma robusta* is dioecious, it has clustered flowers on peduncles 10-15mm and is wind-pollinated and fruits are orange berries, 8-9mm, bird-dispersed. Karamu trees are also found all over ZEALANDIA, mostly studied along the Jim and Eve Lynch Track, Round the Lake Track and Valley View Track.

Hedycarya arborea

Hedycarya arborea commonly known as Pigeonwood (family Monimiaceae), is the only species of *Hedycarya* in New Zealand. It is also a common tree species in lowland and mountain forests. It grows up to 16 m high and 50 cm in diameter. Pigeonwood has thick leathery leaves 5-12.5cm long and 2-3cm wide with coarse serrated margins. It is also a dioecious species, flowers are lightly green, very fragrant, 6-10mm diameter and fruits are bright orange berries about 1cm long. Pigeonwood flowers are insect pollinated and fruits are bird dispersed. Pigeonwood trees are mostly found in north facing forest overlooking the upper lake and lower lake in ZEALANDIA and were studied mostly along the Round the Lake track and Fantail Track.

Macropiper excelsum

Macropiper excelsum (common name Kawakawa, family Piperaceae), is an understorey shrub found commonly in lowland and coastal forests with milder climates. It grows as a small tree up to 5m tall with no well-defined trunk most of the time. The leaves are heart shaped dark green shiny with smooth margins, 5-10cm long and 6-12cm wide. The leaves often have holes caused by the caterpillars of a native moth species, *Cleora scriptaria* that feed specifically on kawakawa leaves (see Dawson & Lucas, 2000). Kawakawa are dioecious, the flowers are minute and numerous on a short auxiliary stalk, up to 1.5cm long and 60cm in diameter. The fruits are small orange berries on erect stalks dispersed by birds. In ZEALANDIA, Kawakawa trees were studied along the Round the Lake track and Valley View track.

Melicytus ramiflorous

Melicytus ramiflorous (common name Mahoe, family Violaceae) is an endemic small tree found throughout lowland to lower mountain New Zealand forests. It can grow up to 10m with up to 60cm trunk diameter. Leaves are dark-green, serrated 5-15cm long and 3-5cm wide. Mahoes are dioecious, flowers are small yellow 3-4mm diameter in clusters and fruits are striking violet berries 4-5mm long. The flowers are insect pollinated and fruits are dispersed through frugivory. In ZEALANDIA, Mahoe trees are commonly found along the Valley View track and the Round the Lake track.

Myoporum laetum

Myoporum laetum (common name Ngaio, family Myoporaceae) is a coastal salt-tolerant native shrub or small tree which is found in lowland forests. It can grow up to 10m tall and 30cm diameter. It has glossy leaves with prominent oil glands, 4-10cm long and 2-3 cm wide. Ngaios are distinguished by their dark brown, very sticky leaf buds. The flowers are white with purple spots 2-6 flowered clusters and bird-pollinated and fruits are red to purple berries, 6-9mm long bird-dispersed. In ZEALANDIA, Mahoe trees were mostly studied along the Valley View track.

Pseudopanax arboreus

Pseudopanax arboreus (common name Five-finger, family Araliaceae) is a native bushy tree up to 8m tall found commonly in coastal to mountain forests. It has distinctive composite leaves with fans of five to seven glossy green and serrated leaflets, up to 20cm long and 7 cm wide. The plants are dioecious and the flowers are small brown-

purple in hemispherical clusters pollinated by insects and birds. The fruits are dark purple to black berries dispersed by birds. Five-finger trees are widespread in ZEALANDIA, and were studied along the Valley View track.

Schefflera digitata

Schefflera digitata (common name Pate, family Araliaceae) is also a widespread native tree species found throughout in New Zealand lowland to mountain forests. It grows up to 8m tall with composite leaves of seven thin finely-toothed leaflets, up to 20cm long and 8cm wide. The flowers are clustered inflorescences branched out at the stem tips to many stalks with small green to yellow flowers. The fruits are purple berries dispersed by birds. In ZEALANDIA, Pate trees were mostly studied along the Round the Lake track.

2.3 Phenological methods

There are numerous ways of quantifying phenological patterns. A simple method is to note presence or absence of each phenological event, such as new leaves, open flowers or ripe fruits. This method provides little quantitative description and does not provide comparable data or information on the intensity of phenological events. Researchers have often used the direct count method to estimate intensity of individual phenological events, such as counting all fruits or flowers on small trees, or counting all accessible fruits below a certain height, or counting all fruits on marked branches. In addition to direct counts, intensity scales have been used to record the timing and abundance of phenological events. The scales can vary from subjective such as 'none, some, many' (Lee et al., 1997), to categorical, either using count categories, e.g. 0, 1-10, 11-50, 51-100, >100 fruits (Ehrlén & Eriksson, 1993), or percentage categories, e.g. 0%, 1-25%, 26-75%, 76-100% of canopy area bearing fruit (Wheelwright, 1985). These methods are useful for plants with visible and observable canopies and allows comparison between individuals and species.

Trees and species to be studied can be sampled using different techniques such as random sampling, using transects and/or marking trees. Following fixed transects allows the repeated observations of the same individuals along the transect displaying different phenological events. Also marking the individual trees along the transects allows detailed surveillance of marked individuals of different species growing along the transects. The number of individuals to be studied for phenological observations usually ranged between 5-10 individuals in phenological researches (e.g. Frankie et al., 1974; Wheelwright, 1986; Keeler-Wolf, 1988; Setterfield & Williams, 1996).

The main aims of the fieldwork for this study were to describe the vegetative and reproductive phenologies of some common tree species in ZEALANDIA. Established walking tracks within ZEALANDIA were used as transects to access and observe the study species. All transects were studied on the same day to eliminate the possibility of atypical phenologies being recorded. All the selected individual trees were broadly in a similar regenerating native forest cover, in this case coastal broadleaf-conifer forest. Initially, a pilot survey was conducted to locate and select healthy mature individual trees visible and accessible from walking transects. To ensure representative sampling along a transect, trees were marked at least five metres apart, more often at greater distances. Sampling methodology was consistent between all transects, as was the range of species monitored. The number of species and number of individuals ultimately selected was determined to allow all phenological observations within same day for all plants studied. Time and logistics further limited the number of species that could be studied.

In this study, phenological records were used to collect information firstly on timing and duration of major phenological events of leaves, flowers and fruits and secondly on the seasonal variation in intensity of these events. Following the established walking tracks as transects, I located and marked ten individuals of 12 common tree species and later followed them periodically. Sun-exposed mature trees with visible canopies were chosen randomly and marked with flagging tape (Pérez-Harguindeguy et al., 2013; Cornelissen et al., 2003; Wheelwright, 1985). Observations on all the marked individuals were done within one day.

Phenological observations were made for two years (July 2011-June 2013). Observations on phenological phases were carried out fortnightly by noting the following major phenological stages (Campanella & Bertiller, 2008; Chaieb, 1997): 1) presence of flower buds; 2) open flowers prior to anthesis; 3) presence of unripe fruits; 4) presence of ripe fruits; 5) vegetative inactivity; 6) presence of leaf buds (<2mm), 7) presence of newly expanded leaves; 8) leaf abscission. The abundance of each phenological stage on each marked individual was scored by one observer using a subjective four-step scale based on the approximate percentage of canopy covered by each phenological stage: not present (0%), present (1-25%), abundant (>25-75%), very abundant (>75-100%). The leaf abscission phenology however was determined by the same subjective scale of percentage content of freshly fallen leaves on leaf litter under plant canopies. The resultant data were analysed to answer specific research questions in Chapter 3, 4 and 5.

CHAPTER 3

PHENOLOGY OF FLOWERS, FRUITS AND LEAVES

IN A NEW ZEALAND FOREST

3.1 Introduction

Phenology is the study of repeatable phenomena in life cycle events. If quantified for an extended period of time using a standardized protocol, phenological data can provide important information on the structure and function of plant communities. However, field observations of phenological cycles are labour intensive and therefore relatively uncommon.

Phenology of plants can be affected by a number of factors which can be grouped into proximate and ultimate causes (Lobo et al., 2003). Proximate factors include primarily short-term environmental events that trigger certain phenological events, whereas ultimate causes include evolutionary characteristics that shape the phenological pattern. Environmental factors such as water availability, seasonal variations in temperature, rainfall and sporadic climatic events, and photoperiod and irradiance are mentioned to trigger phenological events (Chuine, 2010; Fenner, 1998). On the other hand, biotic factors such as competition for pollinators and dispersers can be the ultimate cause for phenological patterns in some plants (van Schaik et al., 1993). Proximate factors are believed to trigger a phenological event and ultimate factors influence the timing (van Schaik et al., 1993).

The timing and duration of flowering, fruiting and leafing events determine the phenological behaviour of plants. Firstly, the timing of flower production is a key feature affecting successful pollination and seed set. It can influence whether a plant attracts the services of pollinator resources, which are often in limited supply (Elzinga et al., 2007; Newstrom, Frankie, & Baker, 1994). The timing of flower production can also be constrained by climatic factors such as moisture availability and photoperiodicity. In

particular, temperate regions typically have shorter periods of favourable climatic conditions for pollination. Flowering often occurs in spring, at the outset of benign climatic conditions, and before canopy closure which shades flowers from ectothermic pollinators in certain deciduous species (Kudo, Ida, & Tani, 2008; Totland, 1993; Heinrich, 1976).

Likewise, the timing of fruit production can influence seed production, rates of seed germination and seedling survivorship (Griz & Machado, 2001; Newstrom et al., 1994; Rathcke & Lacey, 1985). Though peak fruit production may differ greatly with latitude, Ting et al. (2008) showed a general tendency for annual fruit production to peak 2 months after peak periods in annual productivity, with the length of fruiting seasons increasing towards the equator. Fruit phenologies can also vary with modes of seed dispersal. Wind-dispersed species often set fruit during drier periods to facilitate effective wind dispersal (Tackenberg et al., 2003). On the other hand, the fruit phenologies of animal-dispersed species may often coincide with wetter periods to enhance seed germination (Schupp, 1993).

Vegetative phenologies operate differently from flower and fruit phenologies, because they are comprised of two distinct processes, the production of new leaves and the abscission of old leaves. Furthermore, leaf production and abscission phenologies are often associated with different environmental conditions (Kikuzawa & Lechowicz, 2011; Wright et al., 2004; Noma & Yumoto, 1997; Kikuzawa, 1983). The timing of leaf production often coincides with increases in temperature and productivity in spring (Menzel et al., 2006; Larcher, 2003). To avoid the influence of harsh climatic conditions, periods of leaf abscission often coincide with the onset of harsh environmental

conditions in winter, which are particularly visible on deciduous trees (Menzel, 2000). In a seasonal climate, the onset of winter brings a decrease in insolation and sunshine hours, a decline in temperature, and a wet and disturbed environment. Additionally, climatic extremes such as frost, high wind and drought may trigger leaf senescence and abscission (Vincent 2006).

Past work on plant phenologies in New Zealand has been conducted in several localities across the country (Fitzgerald, 1976; Wardle & Campbell, 1976; Clarke, 1968; Scott, 1960). Previous phenological observations have also focused on plant reproductive phenologies, and in particular, how flower and fruit phenologies affect foraging patterns of pollinators and dispersers (Cummings et al., 2014; Dijkgraaf, 2002; Perrott & Armstrong, 2000; O'Donnell & Dilks, 1994). Vegetative phenologies have been mostly limited to deciduous species (Dungan et al., 2004; McGlone et al., 2004; Dungan et al., 2003). Fewer studies have quantified reproductive and vegetative phenologies jointly to provide a more holistic picture of phenological cycles in New Zealand plant communities.

We conducted phenological observations on 12 common plant species in a conifer-broadleaf forest on New Zealand's North Island for two successive years. Data were used to test five predictions: 1) flowering occurs in spring, coincident with rising spring temperatures, 2) fruiting occurs in summer, coincident with annual peaks benign climatic conditions, 3) leaf production occurs in spring, coincident with the onset of benign conditions for photosynthesis, 4) leaf abscission occurs in early winter, coincident with onset of harsher winter conditions, and 5) flower, fruit and leaf

phenologies occur at similar times between years, 6) phenological dispersion and seasonality differ between phenological events each year.

3.2 Methods

Phenological observations of flowers, fruits, and leaves were made on 10 individuals of the 12 of the most common plant species in 'ZEALANDIA' as described in section 2.3. Observations on phenological phases were carried out fortnightly by noting the following phenological stages: 1) presence of flower buds, 2) open flowers prior to anthesis; 3) presence of unripe fruits, 4) presence of ripe fruits, 5) vegetative inactivity, 6) presence of leaf buds (<2mm), 7) presence of newly expanded leaves, and 8) leaf abscission (following Campanella & Bertiller, 2008; Chaieb, 1997).

The abundance of each phenological stage on individually marked trees was scored into one of four categories based on the approximate percentage of canopy covered by each phenological stage: not present (0%), present (1-25%), abundant (>25-75%), very abundant (>75-100%). The leaf abscission phenology was determined by observing percent coverage of freshly fallen leaves on the forest floor under plant canopies along all transects studied. Plant canopies and canopy floors were observed at the same time. All freshly fallen leaves whether young, mature or senesced were recorded as leaf abscission. The number of individuals/species displaying each phenological event for this chapter was compiled from the abundant and very abundant categories. The interspecies as well as the intraspecies values of monthly distributions demonstrating each phenological event were then used to determine peak phenological timing for each species, as well as peaks in the major phenological events.

Flower, fruit and leaf phenologies were quantified as annually repeating, circular variables. Mean monthly abundances of open flowers, ripe fruits, newly expanded leaves and freshly fallen leaves were tallied among marked plants for each species following Zar (1996) using months as angles from 0° to 360° at 30° intervals (e.g., 0°-30° is January, 330°-360° is December, etc.). Annual averages were calculated as the peak date and standard deviations were calculated as the length of mean vector (r).

To test whether phenological events were significantly 'seasonal', I conducted Rayleigh's tests of uniformity on monthly distributions of the number of species flowering, fruiting, producing new leaves and abscising old leaves. While basic Rayleigh's tests of uniformity establish whether each phenological event was clustered within certain times of the year, they do not test our *a priori* predictions for the timing of each phenological (Ruxton 2017 *in press*; Lund et al. 2013). To test hypotheses for the timing of phenological events, I conducted Rayleigh's test of uniformity with specified mean directions (μ). I predicted flowering and leaf production to occur at the onset of benign growing conditions in spring, i.e. September ($\mu=285°$). I predicted fruit production to occur two months after annual peaks in productivity in February ($\mu=45°$) following Ting et al. (2008). Lastly, I predicted leaf abscission to occur at the onset of harsh winter conditions, i.e. June ($\mu=195°$). To test whether phenological events occurred at similar times among years, I conducted a Watson's two-sample test of homogeneity (see Zar, 1996). Additionally, to test the equality of mean vectors of phenological events and their dispersions, Rao's test for homogeneity was performed (Tasdan & Yeniay, 2014; Jammalamadaka, Rao & SenGupta, 2001). All calculations and analyses were carried out in R v.3.0.2 (R Foundation for Statistical Computing, 2014) in the package *Circular* (Lund et al., 2013).

Actual evapotranspiration, which serves as a proxy for primary productivity, is an amalgamation of temperature, precipitation and solar radiance (Ting, Hartley, & Burns, 2008). Wellington, being close to Cook Strait which connects the Tasman Sea with the South Pacific Ocean, faces fluctuations in oceanic oscillations, solar cycles and circulation patterns, as well as a high frequency of strong winds (NIWA, 2014; Badeck et al., 2004). Wellington had the largest average annual highest maximum wind gusts (averaging 142 km/hr from 1972 to 2016) of all New Zealand locations with six or more years of data (Ministry for the Environment, 2015). Thus, to evaluate the climatic drivers of each phenological stage, mean monthly values of rainfall, sunshine, temperature and wind speed were obtained online from Karori East weather station (www.harvest.com) and a database of NIWA (National Institute of Water and Atmospheric Research) (NIWA, 2014). Patterns in plant phenologies were then compared to climatic variables graphically to identify the climatic conditions coincident with each phenological stage (Fig 3.1).
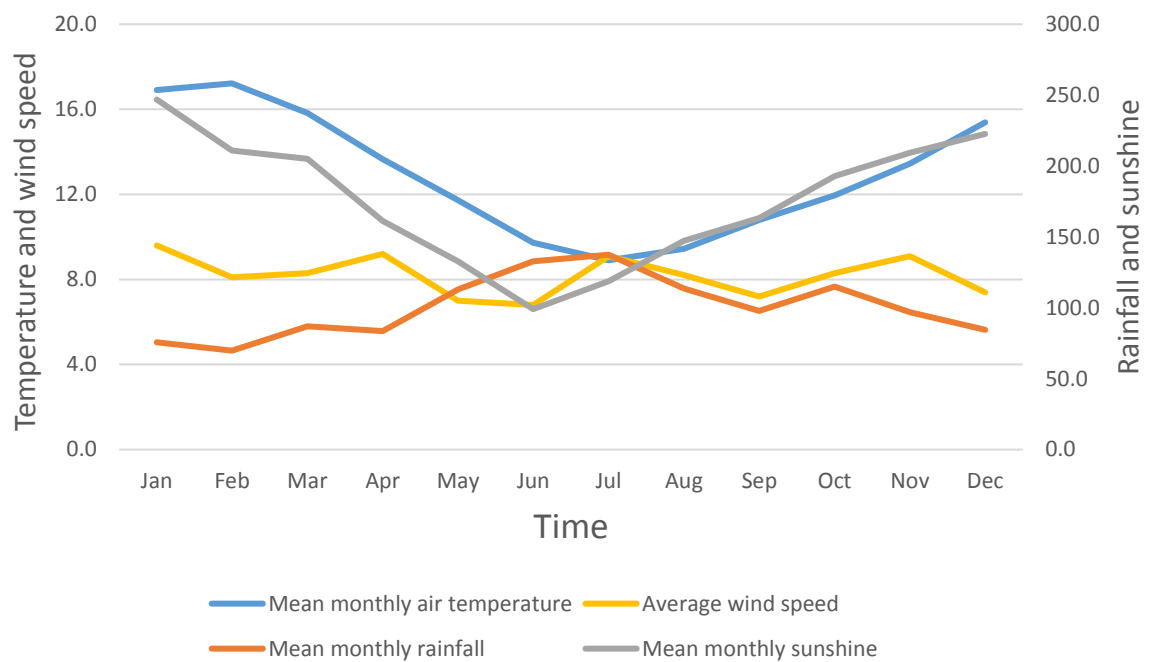
Figure 3.1 The annual variation in mean monthly rainfall (mm), sunshine (hours), air temperature (°C) and wind speed (km/hr) for the year 2013.

3.3 Results

The phenologies of flowers, fruits and leaves were clustered into distinct 'seasons' (Fig. 3.2). The length of the mean circular vector (r) differed significantly from uniform annual distributions (flowers, r = 0.60, p < 0.001; fruits, r = 0.55, p < 0.001; leaf production, r = 0.83, p < 0.001; leaf abscission, r = 0.87, p < 0.001). Therefore, all phenologies exhibited a mean vector that was longer than expected by chance, indicating pronounced seasonality in reproductive and vegetative phenologies.

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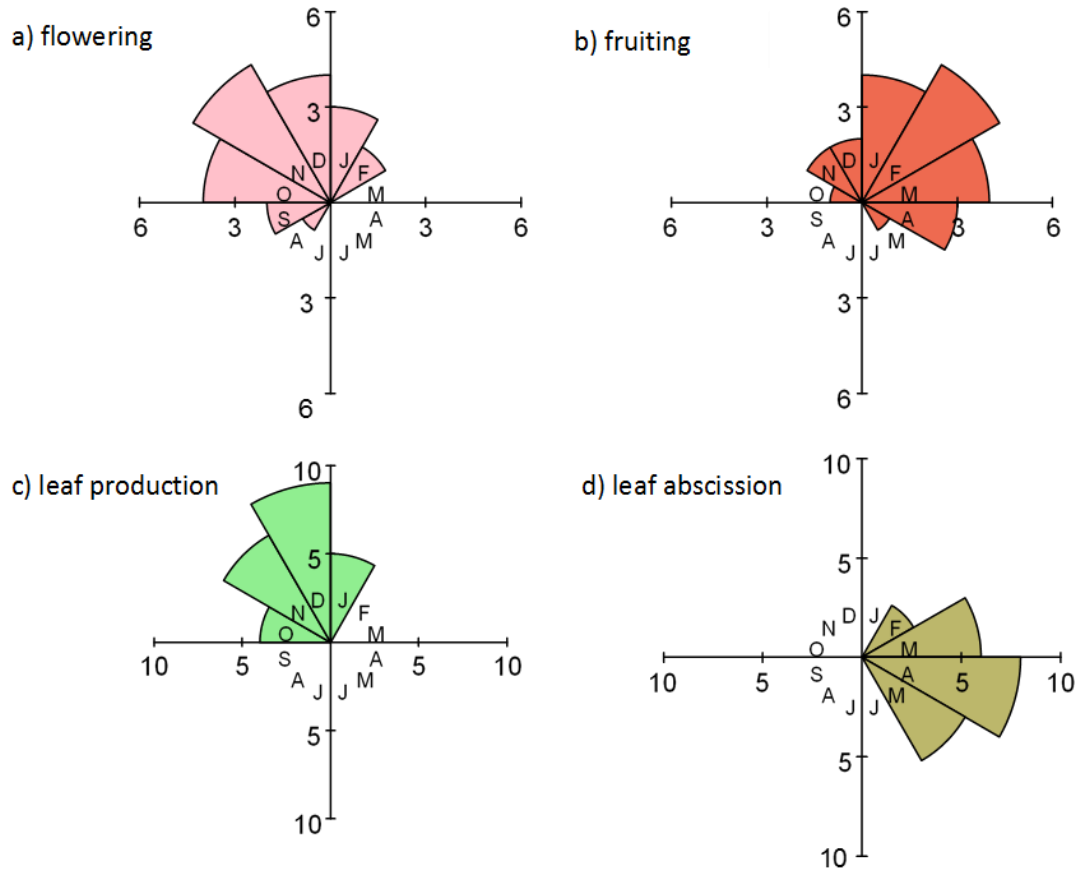
Figure 3.2: Rose diagrams representing annual variation in flower, fruit and leaf phenologies for the year 2012. Bins represent monthly variation in the number of species a) flowering, b) fruiting, c) producing new leaves, and d) absicissing leaves throughout the year.

Flowers and new leaves were produced in late spring (flowers: mean angle = 323.56°, i.e. mid-November; leaf production: mean angle = 332.14° i.e. early December), which was significantly later than my predictions that they should occur at onset of benign climatic conditions in September (flowers: test statistic (r) =0.55, p<0.001 at μ=285°; leaf production: r=0.58, p<0.001 at μ=285°). Fruit production peaked at the end of summer (mean angle = 42.57°, i.e. mid-February), which was consistent with my prediction that

fruiting peaks should occur two months after annual peaks in productivity (r=0.62, p<0.001 at μ=45°). The annual peak in leaf abscission occurred in autumn (mean angle: 96.82°, i.e. April) prior to my prediction that it should occur in June (r=-0.109, p>0.05 at μ=195°) (Fig. 3.2, Table 3.1 and 3.2).

The timing of leaf, flower and fruit phenologies was similar among years (Fig. 3.3, Table 3.1). Results from Watson's two-sample test of homogeneity (circular analogue of a t-test) were significant in all four cases, indicating peak phenological dates of flowers, fruits and leaves did not differ between study years (Watson U^2 < 0.10, p > 0.10). Rao's test for homogeneity showed equality of mean vectors of phenological events (p>.05), however the test rejected the equality of their dispersions (p<0.05), i.e. the dispersions of phenological data significantly differed between the four phenological events.

Table 3.1 Community-level variation in peak timing (circular mean angle) and degree of seasonality of flowering, fruiting, leaf production and leaf abscission phenologies in 2012 and 2013.

2012	Flowers	Fruits	Leaf production	Leaf abscission
Peak date	323.56	42.57	332.14	96.82
Seasonality	0.60	0.56	0.87	0.87
Range	210	240	120	90

2013	Flowers	Fruits	Leaf production	Leaf abscission
Peak date	328.90	45.60	335.21	96.09
Seasonality	0.61	0.53	0.80	0.87
Range	210	240	120	90

Table 3.2 Average phenological peaks (circular mean angle) of the 12 study species between study years. Standard deviations are shown in parentheses.

Species	Average mean angle (degrees)					
	Flowering (a)	Fruiting (b)	Distance (a-b)	Leaf production (c)	Leaf abscission (d)	Distance (c-d)
Fuchsia excorticata	305.27(31.42)	28.60(24.53)	83.33	315.62 (30.38)	105.23 (17.43)	149.61
Geniostoma rupestre	310.44(22.32)	60.77(15.54)	110.33	305.11 (20.56)	89.56 (18.01)	144.45
Macropiper excelsum	278.68(18.49)	325.32(18.49)	46.64	313.10 (22.62)	126.98 (24.05)	173.88
Schefflera digitata	23.53(19.25)	69.23(20.12)	45.7	289.96 (20.36)	105.00 (17.99)	175.04
Aristotelia serrata	308.29(15.39)	43.39(17.71)	95.1	313.17 (15.97)	126.12 (14.75)	172.95
Coprosma grandifolia	320.07(35.04)	55.42(18.72)	95.35	350.92 (19.25)	155.41 (17.01)	164.49
Melicytus ramiflorous	11.98(33.31)	102.67(19.67)	90.69	289.98 (17.81)	94.92 (19.67)	164.94
Hedycarya arborea	350.02(16.59)	30.23(26.00)	40.21	333.23 (15.39)	107.32 (14.67)	134.09
Coprosma robusta	295.46(18.22)	45.77(25.44)	110.31	345.77 (22.03)	140.02 (19.01)	154.47
Myoporum laetum	335.94(22.60)	105.76(19.22)	129.82	336.55 (19.08)	126.38 (20.36)	149.83
Pittosporum eugenioides	315.31(17.22)	65.10(20.11)	109.79	300.69 (22.66)	135.36 (15.33)	194.67
Pseudopanax arboreus	245.77(20.12)	295.19(21.23)	49.42	328.98 (19.92)	123.64 (17.71)	154.66
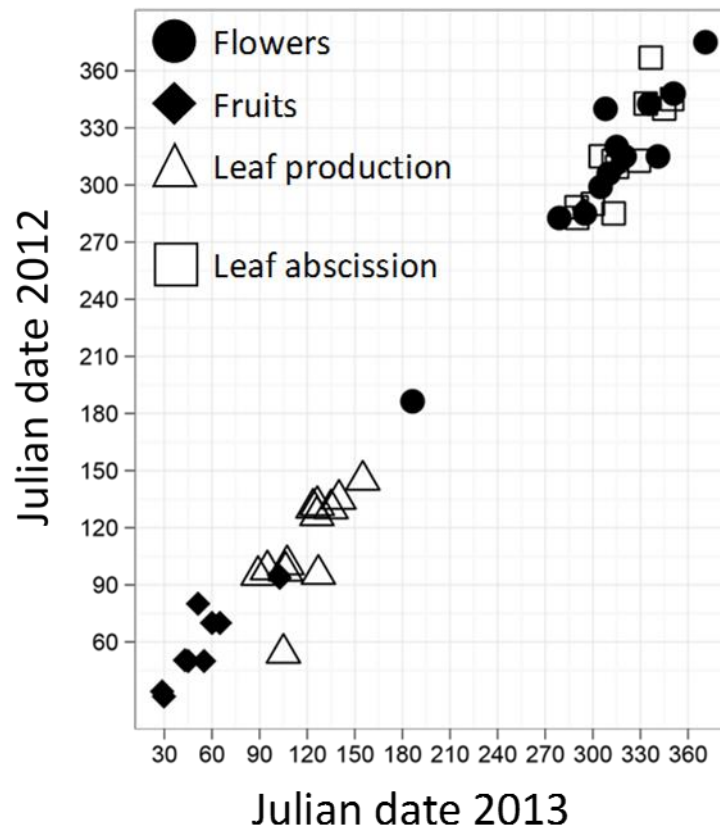
Figure 3.3: Relationship between phenological events in two successive years of observations in 12 study species. Peak Julian dates of flowering (black circles), fruiting (black diamond), leaf production (white triangle) and leaf abscission (white squares) in 2012 (y-axis) are plotted against peak dates in 2013 (x-axis).

3.4 Discussion

The phenology of flowers, fruits, as well as the timing of leaf production and leaf abscission showed pronounced and consistent seasonality. However, flowering phenologies and leaf production periods occurred in late spring, later in the year than I expected. Fruit production occurred in late summer, approximately two months after

the annual peak in productivity. Leaf abscission was concentrated at the end of autumn, prior to the onset of harsher environmental conditions associated with winter, and slightly earlier than I expected.

Seasonality in flower production is often linked with a range of environmental conditions including annual peaks in irradiance, the onset of wet periods and the availability of pollinators and dispersers (Brody, 1997; Murali & Sukumar, 1994; Wright & van Schaik, 1994). Flower phenologies and leaf production phenologies occurred at approximately the same time in spring slightly later than our *a priori* predictions. Community-level peaks in flowering phenologies also occurred before the peak in leaf production, which has been reported previously (Orshan, 1989; Specht & Morgan, 1981). Deciduous trees often produce flowers at the onset of the growing season, which is then closely followed by leaf production.

Ting et al. (2008) showed that on a global scale, community level peaks in fruit phenologies occur approximately two months after annual peaks in productivity. Results reported here are broadly consistent with this finding, as the community-level peak in fruit production occurred in late summer, following annual peaks in temperature and sunshine. Seasonal variation in the abundance and distribution of pollinators and seed dispersers are also known to be associated with flower and fruit phenologies (e.g. Burns, 2003). However, native New Zealand birds are largely non-migratory, and they are present at my study site year-round (Bell, 2015), suggesting that reproductive phenologies are more tightly linked with climate than with seasonal fluctuations in the supply of mutualists.

Many New Zealand birds interact with plants as both pollinators and seed dispersers (Burns, 2013). If selection from animal mutualists were the primary driver of fruit and flower phenologies, then one might predict fruits and flowers to be produced evenly throughout the year. However, results reported here demonstrate clear annual seasonality in fruit and flower availability. Flowers and fruits are produced in abundance at specific times of year, spring and summer respectively, followed by a pronounced period of fruit and flower scarcity in winter. Perrott and Armstrong (2000) also noted limited food availability for native birds during autumn and winter (see also O'Donnell & Dilks, 1994; Bell, 1982).

Leaf phenologies are an important driver of ecosystem productivity and nutrient cycling. Leaf production is usually linked to spring warming and photoperiodicity (Kikuzawa, 1983; Lechowicz, 2001). Seasonality in climate in temperate regions results in temporally restricted growing seasons. As a result, plants aggregate leaf production periods at the outset of benign growing seasons to maximize carbon. Although later than I predicted, the results showed that leaf production times broadly coincide with the onset of favourable climatic conditions in late spring, which are characterised by rising temperatures, greater amounts of sunshine and lower precipitation. However, the study species that produced leaves at the same time often differed greatly in their longevities, thereby abscising leaves after varying amount of time, with some species maintaining their leaves for only a few months (e.g. *Fuchsia excorticata*), while others maintained leaves for over three years (Paudel, 2017 *unpubl*.).

After a period of successful photosynthetic return, leaves senesce and eventually abscise (Kikuzawa & Lechowicz, 2011; Vincent, 2006). Leaf abscission prior to the outset

of poor growing conditions may help plants conserve energy during periods of lower productivity and declining photosynthetic return (i.e. winter). Leaf abscission in late autumn might also help plants recover their nutrient investments in leaves, which might get damaged during strong winter storms. Although I found distinct seasonality in leaf abscission times, other temperate regions show interspecific differences in leaf abscission times (Polgar & Primack, 2011; Lechowicz, 1984). As a result, despite pronounced seasonality in both leaf production times and leaf abscission times, most species were 'evergreen', displaying multiple annual cohorts of leaves simultaneously.

The climate is warming, approximately by 0.6°C over past 100 years (IPCC, 2013). The responses of the changing climate are visible in, for example, the phenology of organisms, their physiology, the distribution of species and their interactions, compositions and structure within communities (Visser & Both, 2005; Dunn, 2004, Parmesan & Yohe 2003; Root et al., 2003; Walther et al., 2002; Hughes, 2000). Phenology provides a simple way to evaluate these responses and to better understand the effects of changing climate (Walther et al., 2002). Rising temperature is evidenced to alter the timing of plant phenology, for example earlier occurrence of spring activities such as leaf and flower production (Cleland et al., 2007; Visser & Both, 2005; Badeck et al., 2004; Parmesan & Yohe, 2003; Walther et al., 2002). The highest minimum and maximum temperature for the study area was 1°C higher in 2013 than it was in 2011, which is 1°C rise during the study duration (Fig. 3.4). Overall results provide base line information on seasonal phenological patterns in some common New Zealand plant species with implications for future climate change research.
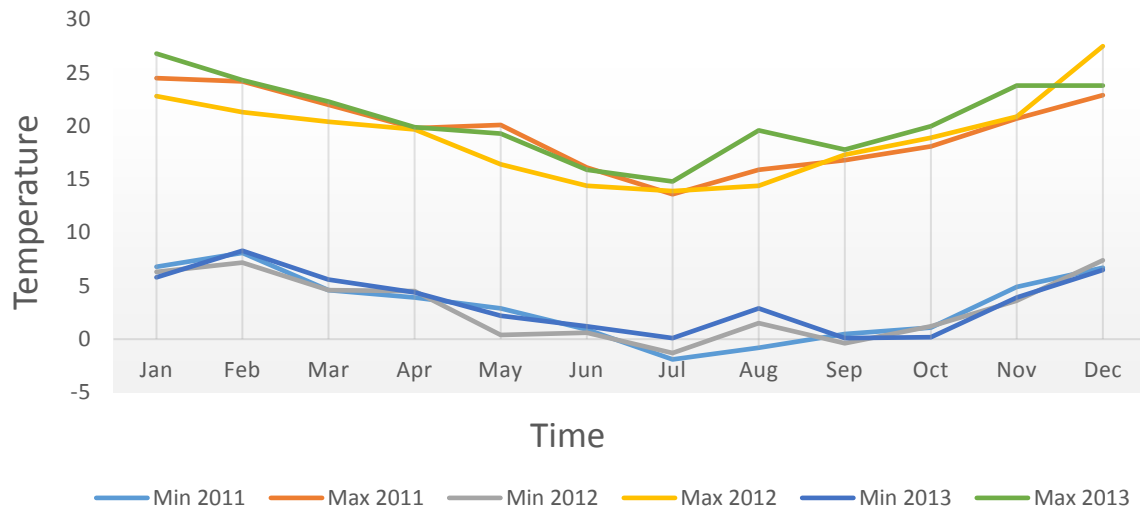
Figure 3.4 The annual variation in mean monthly minimum and maximum temperature for the year 2011, 2012 and 2013 from Karori East Station at 190 (SID: 1278).

Overall results from this study showed that both reproductive and vegetative phenology events showed strong, consistent seasonality. Although many of my specific predictions were not supported by the results, all phenological events corresponded broadly with annual changes in climate. Future long-term observations may help to elucidate more definitive relationships between phenological events and climate, and how plant phenologies vary between years and across broad spatial scales. A more thorough understanding of the climate-phenology relationships is a necessary first step towards understanding how New Zealand forests will respond to global climate change.

CHAPTER 4

CLIMATIC EFFECTS ON LEAF LONGEVITY:

HOW IMPORTANT IS LEAF ECONOMICS?

4.1 Introduction

Vegetation types are often delineated by community-level patterns in leaf longevity. Temperate 'deciduous' forests get their name from tree species that produce and abscise leaves at specific times of year, leading to strong seasonality in forest productivity. On the other hand, 'evergreen' forests are comprised of species that maintain functional leaves year-round. Community-level patterns in leaf longevity can be quite complex. For example, some evergreen species produce and abscise leaves continuously, while others produce and abscise leaves in unison, but retain leaves for longer than a year (Kikuzawa & Lechowicz 2011). Given its importance to the structure and function of pant communities, understanding community-level patterns in leaf longevity is a central goal of plant ecology (Chabot & Hicks 1982; Reich et al. 1992).

Recent work on relationships among leaf traits has greatly improved our understanding of interspecific variation in leaf longevity (Wright et al., 2004; Heberling & Fridley 2012; Funk & Cornwell 2013; Díaz et al., 2015). Across the globe, leaf longevity is correlated with leaf mass per unit area (LMA), photosynthetic rate and several other leaf traits that have important physiological functions (Wright et al., 2004). This 'leaf economic spectrum' therefore represents a single axis of trait variation among plant species. At one end of the spectrum, species have short-lived, low mass per unit area leaves with higher nutrient content and faster rates of photosynthesis. At the other end of the spectrum, species have longer-lived, higher mass per unit area leaves with lower nutrient content and slower rates of photosynthesis (Wright et al., 2004). As a result, species with long leaf longevities typically have a 'slow' life history strategy, while species with short leaf longevities have a 'fast' life history strategy.

In addition to being linked to 'slow' versus 'fast' life history strategies, leaf longevities might also be influenced by seasonality in leaf abscission and leaf production times, both of which are known to be influenced by climate (Chuine & Cour, 1999; Kudo et al., 1999; Lechowicz, 2001; Badeck et al., 2004; Cleland et al., 2007). The initiation of leaf production is often associated with temperature (Lechowicz, 2001), and leaf elongation can be related to irradiance, as well as other factors (Larcher, 2003). On the other hand, climatic extremes such as frost, high winds or drought may trigger senescence (Visser & Both, 2005). Previous work on the relationship between climate and leaf longevity has focused on the onset of bud break times in spring and how they might vary with global climate change (Ahas, 1999; Beaubien & Freeland, 2000; Ahas et al., 2002; Buitenwerf et al., 2015). On the other hand, leaf abscission times have received less attention and may be more difficult to predict (Menzel, 2000).

In aseasonal tropical environments, leaves are exposed to similar climatic conditions throughout the year, regardless of when they are produced. However, few places on earth are truly aseasonal. Therefore, as leaf lifespan increases, so does the possibility that they will experience seasonal variation in climatic conditions that limit their physiological performance. Climatic constraints on leaf performance vary markedly with latitude (Lechowicz, 2001; Chuine & Cour, 1999). At high latitude sites, periods of benign climatic conditions for plant growth are comparatively short, and as latitude declines, climatic constraints on leaf longevity tend to diminish. Correspondingly, as climatic seasonality increases, the prevalence of broad-leaved evergreen forest tends to decline, while deciduous forest increases (Kikuzawa, 1991). However, southern hemisphere

forests, such as in New Zealand, are predominantly evergreen, despite pronounced seasonality in climate (McGlone et al., 2010; Buitenwerf et al., 2015).

Here, I explore the relative influence of climate and leaf trait correlations on leaf longevities in a south temperate forest in New Zealand. I observed leaf production times, leaf abscission times and leaf retention times in 12 common broadleaved tree species to test whether: 1) leaf longevities increase with leaf mass per unit area, an easily measured trait that is often used to determine a species' position along the leaf economics spectrum, 2) periods of leaf production and abscission are uniformly distributed throughout the year, or instead, whether they show significant temporal clustering associated with seasonal variation in climate, (3) seasonal trends in leaf production and abscission were consistent between years, and hence (4) how seasonality in leaf production and abscission times interact with leaf mass per unit area to determine community-level patterns in leaf longevity.

4.2 Methods

Leaf mass per area versus leaf longevity

Leaf longevity was measured in the 12 most common woody broadleaf plant species in ZEALANDIA (Section 2.1, Table 4.1) by marking five newly produced leaves from 10 individuals of each species. The first expanded leaf from a marked leaf bud was marked with green duct tape loosely on its petiole to allow further growth of the leaf. Sun-exposed leaf buds were selected randomly from mature trees with a visible canopy following a standardized protocol set out in Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013). Five such leaf buds were followed fortnightly between

September 2011 and May 2014 or until they fell off. Leaf longevity was calculated as the time interval separating the emergence of fully expanded leaves and their disappearance from adult trees. Values for each leaf were first averaged within plants, and then among plants, to obtain a single value for each species.

Leaf mass per unit area was measured in all 12 study species following Pérez-Harguindeguy et al., 2013 and Cornelissen et al., 2003. Photosynthetically active (young but fully expanded) leaves from healthy adult plants were selected randomly from the sun-exposed outer canopy. Five newly produced, fully expanded leaves were collected from 10 adult plants (n = 50 leaves per species) from the study area and transferred to the laboratory for measurements. The surface area of each leaf (m^2) was obtained using a Li-Cor 3100 leaf area meter. Leaves were then dried for 48 h at 65° C and then weighed to the nearest gram. Leaf mass per unit area was calculated for each leaf (g/m^2). Values were averaged among leaves within individuals and then among individuals for each species. Pearson's correlation was then used to assess the relationship between leaf mass per unit area and leaf longevity. A General linear model was used to explore variations in leaf longevity cohorts and also to compare bivariate relationship of leaf longevity with LMA between my study and other available datasets.

Seasonality in leaf production and abscission

A second suite of phenological observations were made (as described in Section 2.3) to quantify seasonal variation in leaf production and abscission times. Although ideal for obtaining precise estimates of leaf longevity, observations of individually-marked leaves were less useful in quantifying annual patterns in leaf productions and abscission times,

as well as determining whether these times occurred consistently among years. To quantify seasonal patterns in leaf production and abscission, 10 mature trees with clear visual access into their canopies were marked and censused at fortnightly intervals between September 2011 and May 2014. During each census trees were classified as belonging to one of three phenological stages for the purpose of this chapter: (1) presence of newly developing leaves, (2) presence of leaves in the process of abscission, (3) vegetatively inactive, i.e. neither producing nor abscising leaves.

To test for significant seasonality in leaf production and leaf abscission times, leaf phenologies were quantified as annually repeating, circular variables. Mean monthly abundances of newly expanded leaves and freshly fallen leaves were tallied among marked plants for each species following Zar (1996) using months as angles from 0° to 360° at 30° intervals (e.g., 0° - 30°, referring to January; 330°-360° referring to December). Annual averages were calculated as the length of mean vector (r).

To test whether phenological events were significantly 'seasonal', I conducted Rayleigh's tests of uniformity on monthly distributions of the number of species observed to be producing new leaves and abscising old leaves. All analyses were conducted in R v.3.0.2 (R Foundation for Statistical Computing, 2014). Circular statistics were conducted with the package Circular. I also conducted Watson's two-sample tests of homogeneity (circular analogue of a t-test) to evaluate whether leaf production and leaf abscission times were consistent among years.

4.3 Results

Leaf longevity varied widely among species, from 6 months to over 30 months (Fig. 4.1). Three leaf longevity categories were apparent. One species abscised its leaves approximately six months after they were produced (*Fuchsia excorticata*). Six species abscised their leaves approximately 18 months after they were produced (*Geniostoma rupestre*, *Macropiper excelsum*, *Schefflera digitata*, *Aristotelia serrata*, *Coprosma grandifolia* and *Melicytus ramiflorus*) and three species abscised leaves approximately 30 months later (*Hedycarya arborea*, *Pittosporum eugenioides* and *Myoporum laetum*). However, one species (*Pseudopanax arboreus*) retained most of its marked leaves at the close of observations, indicating that its average leaf longevity was actually greater than 30 months.

Average values of leaf longevity were correlated with average values of LMA (r = 0.87), indicating that leaves with higher dry mass per unit area were retained on parent plants for longer than leaves with lower leaf mass per area. However, distinct clusters of leaf longevity (6 months, 18 months and 30 months) are apparent from the relationship between leaf longevity and leaf mass per area (Fig. 4.2), which arose from strong seasonality in leaf abscission times. The within cohort variation of 12-18 months and 27-30 months also showed highly correlated bivariate relationship between leaf longevity and LMA (P<0.01, R^2 = 0.94).
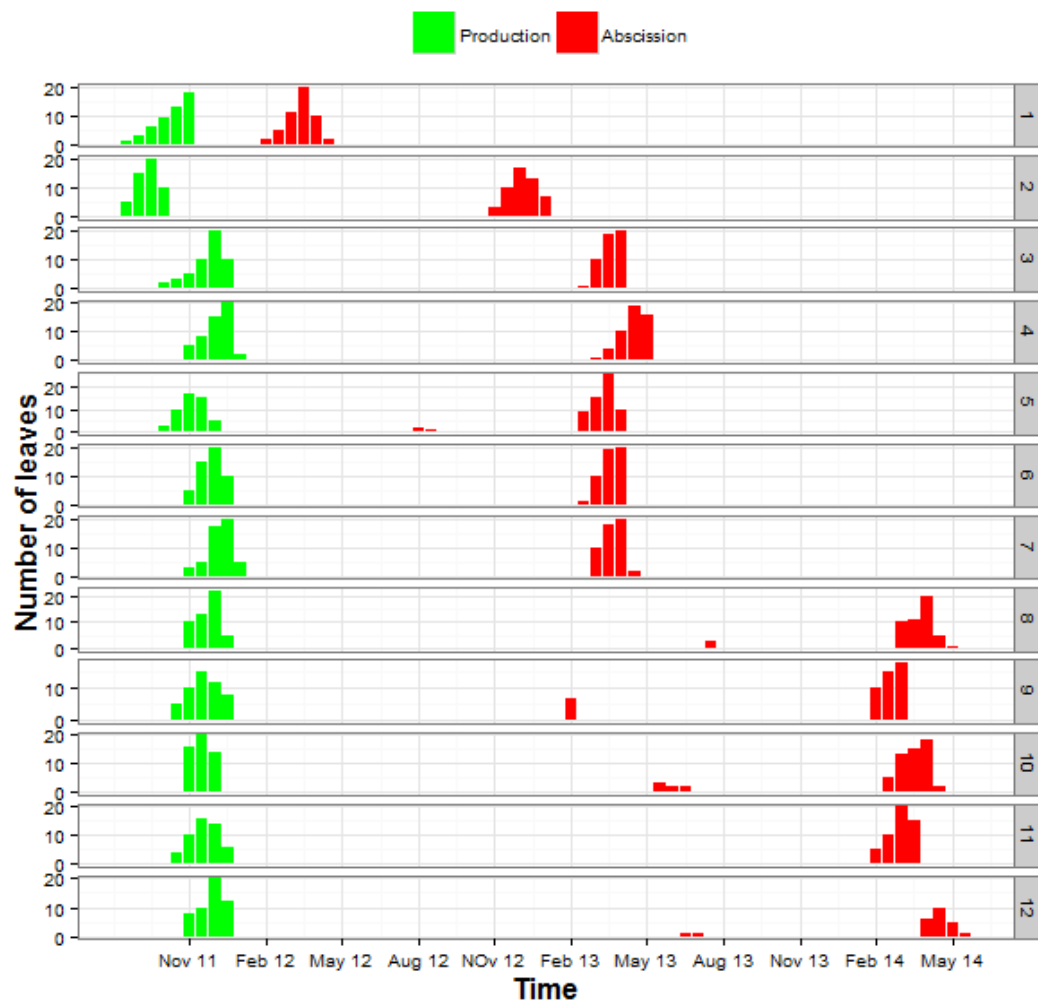
Figure 4.1 Annual patterns in leaf production (green bars) and abscission (red bars) in 12 woody-plant species labelled numerically as in Table 4.1. Bars represent frequencies of marked leaves unfolded and abscised over time.

Leaf production and leaf abscission times were strongly seasonal (Fig. 4.3). Leaf production times were not uniformly distributed throughout the year (p < 0.001, length of mean vector = 0.77). Instead, new leaves were produced in spring (circular mean angle 332.14°, early November) at the onset of benign climatic conditions of rising temperature and sunshine hours. Leaf abscission times were also not uniformly

distributed throughout the year (p < 0.001, length of mean vector = 0.87). Leaf abscission

times were instead clustered in autumn (circular mean angle 96.82°, early-March), prior

to the onset of low temperatures in winter (July). Seasonal trends in leaf production and

leaf abscission times were also consistent among years (Fig. 4.3). Watson's two-sample

test of homogeneity showed that peak phenological dates of leaf production and

abscission did not differ between years (Watson U^2 < 0.10, p > 0.10 in both cases).
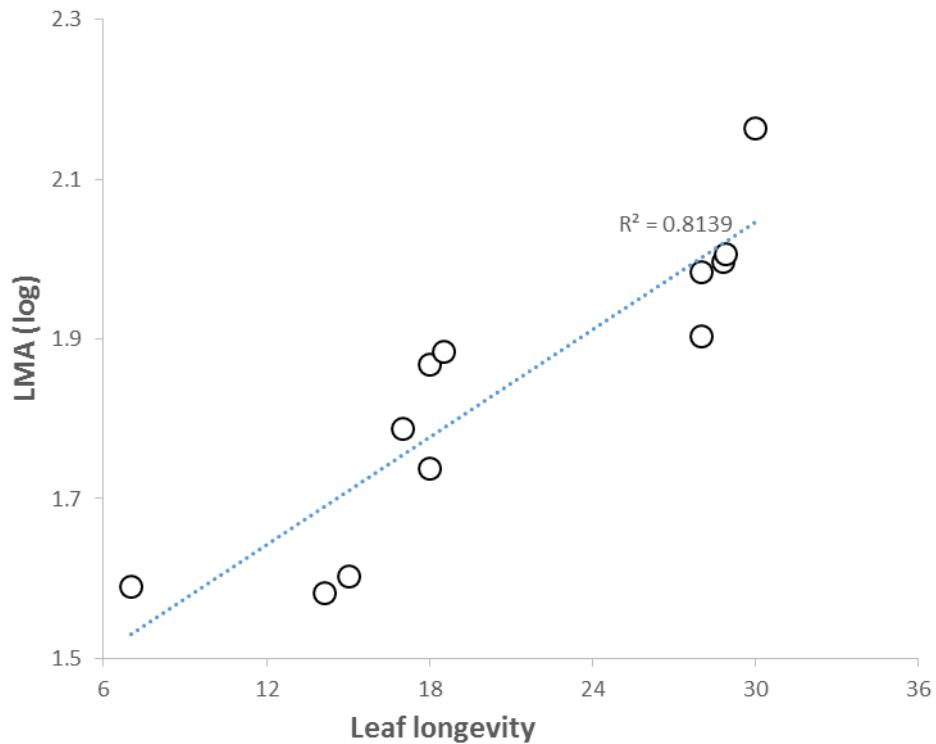
Figure 4.2 Positive relationship between leaf longevity (months) and leaf mass per unit

area (log-transformed, gm/m^2) in 12 woody-plant species.
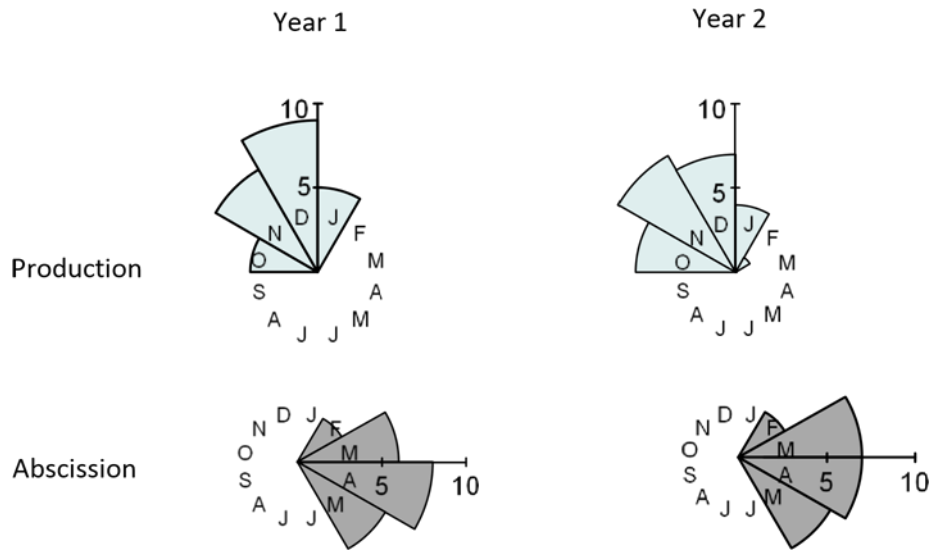
Figure 4.3 Rose diagrams illustrating seasonal patterns in leaf production (top) and leaf abscission (bottom) in the first (left) and second (right) years of study obtained from individually marked trees of 12 woody-plant species. Bins illustrate the number of species producing and abscising leaves each month. Inner circles of letters represent annually repeating months from January to December.

Table 4.1 Average leaf longevity (months), LMA (gm/m^2), average annual peaks (i.e. circular mean angles) in leaf production and leaf abscission in 12 woody plant species from New Zealand. Standard deviations are shown in parentheses. Species are labeled numerically as in Figures 4.2 by the increasing order of leaf longevities. Deciduous species marked with *.

Study species	Leaf longevity	LMA	Mean angles	
			Production	Abscission
1. *Fuchsia excorticata* *	7.00 (± 0.82)	38.24 (± 8.49)	315.62 (± 30.38)	105.23 (± 17.43)
2. *Geniostoma rupestre*	14.10 (± 1.20)	39.01 (± 2.91)	305.11 (± 20.56)	89.56 (± 18.01)
3. *Macropiper excelsum*	15.33 (± 0.63)	40.08 (± 3.97)	313.10 (± 22.62)	126.98 (± 24.05)
4. *Schefflera digitata*	18.00 (± 0.70)	54.78 (± 20.305)	289.96 (± 20.36)	105.00 (± 17.99)
5. *Aristotelia serrata*	17.50 (± 1.27)	61.46 (± 10.29)	313.17 (± 15.97)	126.12 (± 14.75)
6. *Coprosma grandifolia*	18.00 (± 1.50)	73.87 (± 13.70)	350.92 (± 19.25)	155.41 (± 17.01)
7. *Melicytus ramiflorus*	18.50 (± 1.79)	76.71 (± 7.48)	289.98 (± 17.81)	94.92 (± 19.67)
8. *Hedycarya arborea*	28.10 (± 0.96)	80.24 (± 24.45)	333.23 (± 15.39)	107.32 (± 14.67)
9. *Coprosma robusta*	28.23 (± 1.20)	96.67 (± 10.37)	345.77 (± 22.03)	140.02 (± 19.01)
10. *Myoporum laetum*	28.80 (± 0.84)	99.46 (± 11.81)	336.55 (± 19.08)	126.38 (± 20.36)
11. *Pittosporum eugenioides*	28.90 (± 0.63)	101.05 (± 18.38)	300.69 (± 22.66)	135.36 (± 15.33)
12. *Pseudopanax arboreus*	30.00 (± 1.30)	146.16 (± 11.36)	328.98 (± 19.92)	123.64 (± 17.71)

4.4 Discussion

Leaf longevities varied widely among species. Most study species retained multiple cohorts of leaves year-round, giving rise to an 'evergreen' forest at the community-level. As predicted, leaf longevities increased with LMA in a manner consistent with the leaf economics spectrum (Wright et al., 2004). However, leaf production and leaf abscission times showed marked seasonality. Leaf production occurred between October and January, coinciding with the onset of benign growing conditions in spring and summer. Leaf abscission occurred between February and May, coinciding with declining temperatures associated with the approach of winter. Seasonal periods of leaf production and abscission were also highly consistent, between years. These patterns were also consistent for production and abscission times between individually marked leaves and their respective marked plant canopies. Therefore, while interspecific variation in leaf longevity was primarily associated with the leaf economics spectrum, it also appeared to be constrained by seasonality in climatic conditions.

Most woody plant species in New Zealand are evergreen, which has traditionally been attributed to New Zealand's mild climate and low soil fertility (McGlone et al., 2004). With the exception of one deciduous species (*Fuchsia excorticata*), all of my study species retained their leaves for at least one winter season. Leaf longevities in these evergreen species ranged from 14 to 30 months, which is broadly similar to other temperate evergreen forests (Kikuzawa and Lechowicz, 2011). *Aristotelia serrata* widely reported as semi-deciduous specially in colder areas of New Zealand (Haase 1986; Wardle 1991; Dungan et al. 2003c) displayed leaf longevity of around 18 months and overwintered 47 out of 50 marked leaves. McGlone et al. (2004) mentioned three

annual evergreen species (*Hedycarya arborea*, *Myrsine divaricata*, and *Schefflera digitata*) having less than 16 months of leaf longevities. However, *Hedycarya arborea* and *Schefflera digitata* in my study had leaf longevities of approximately 28 months and 18 months respectively. Richardson et al. (2010) reported six New Zealand tree species had mean leaf lifespans of approximately 12 to 47 months and suggested that leaf lifespans could range between two to three years for similar sites and species. Their study did not include any of the species I studied, however, and two species in the same genera as two in my study (*Coprosma foetidissima* (12.4 months) and *Pseudopanax crassifolius* (47 months)) had widely different leaf longevities from my study.

Strong positive associations between leaf longevity and leaf mass per unit area are consistent with the leaf economics spectrum. Leaves with high leaf mass per area often incur high construction costs and have longer life spans than leaves with low leaf mass per area (Shipley et al., 2014; Wright et al., 2004). Interspecific variability in leaf lifespans observed in this study are clearly linked to a continuum of life history traits that correspond to 'fast' versus 'slow' physiological performance (Reich, 2014). Consequently, differences in leaf longevity may be a by-product of selection on a wide range of other leaf traits with important effects on plant form and function (Díaz et al. 2015). Richardson et al. (2010) compared their leaf longevity from six species sampled along the Franz Josef Chronosequence, New Zealand to Glopnet dataset from Wright et al. 2004 and found an overlap of 12% in range of global distribution of the leaf longevity data. Their data covered the area of leaf economic spectrum displaying long-lived leaves with low nitrogen concentrations. Even though my study did not study nitrogen concentrations, the comparison with the global dataset shows a similar position in the

leaf economic spectrum sampled 8% of the full range leaf longevity values (Fig 4.4). For a given LMA, New Zealand species seems have longer leaf longevity than majority of species studied around the world.
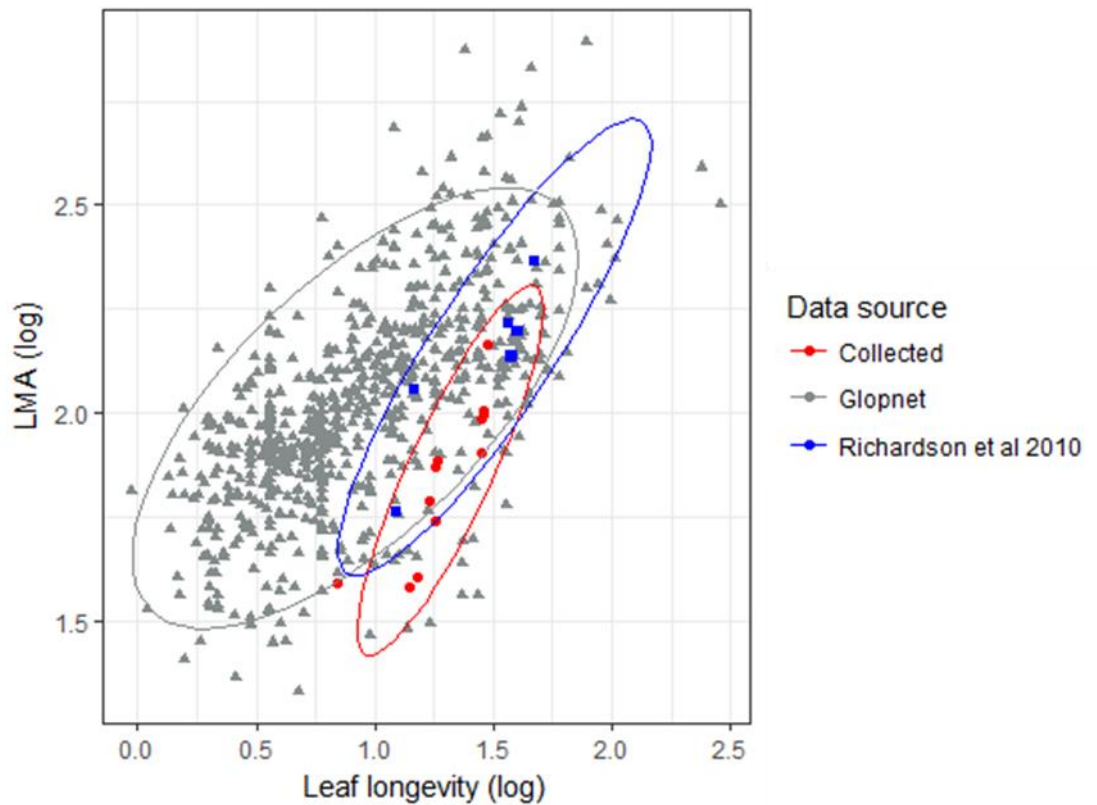
Figure 4.4 Positive relationship between leaf longevity (log, months) and leaf mass per unit area (log, gm/m^2) from a global dataset (Glopnet, Wright et al. 2004) and from species samples from New Zealand including this study.

Climatic controls are a central feature of leaf longevity research (Kikuzawa, 1990, 2003; Richardson et al., 2010; Kikuzawa & Lechowicz, 2011). Every stage in the life of a leaf is regulated, at least in part, by climate. For example, bud break is often associated with spring warming in temperate areas (Lechowicz, 2001) and leaf maturation can be regulated by irradiance levels (Larcher, 2003). Climatic extremes such as frost, high wind

and drought can reduce leaf longevity or trigger senescence (Visser & Both, 2005). Climatic effects could also affect leaf longevity in my study site, where winter brings a decrease in insolation, a decline in temperature and the onset of wet, windy conditions (NIWA, 2014).

Leaf abscission peaked in April, regardless of leaf lifespan. As a result, species fell into distinct categories based on leaf longevity, based on which year their leaves were abscised. Leaf abscission typically occurs in autumn in the Northern Hemisphere, where autumn leaf loss appears to be a strategy for avoiding leaf damage and poor physiological performance during harsh winter climatic conditions (Kikuzawa & Lechowicz, 2011). Leaf abscission occurred in the austral autumn at my study site, between March and May, indicating winter climatic conditions constrain continuous variation in leaf longevity among species.

Leaf production is typically linked to warming and increased photoperiodicity in spring (Bussell,1968; Kikuzawa, 1983; Lechowicz, 2001; Polgar & Primack, 2011). Results reported here support the notion that plants tend to produce leaves at the onset of climatic conditions that are conducive to increased productivity. Strong seasonality in leaf production and leaf abscission times likely create variation in leaf longevities, adding a more categorical pattern, at the same time maintaining a positive relationship with LMA.

Research into the leaf economics spectrum illustrates that plant species worldwide conform to a continuum of life history variation, from slowly developing, long-lived leaves in some to fast developing, short-lived leaves in others. The positive association between leaf mass per unit area and leaf longevity observed here suggests a similar life

history strategy within my study species, so they also conform to the leaf economics spectrum. However, strong seasonality in leaf production and leaf abscission times, corresponding to climatic conditions that are conducive and detrimental to plant productivity, respectively, suggest that leaf longevity is also constrained by climatic seasonality (see also Wright et al., 2005). Overall results therefore contribute to a growing body of recent research highlighting additional contributing factors to leaf trait co-variation in plants, plant defensive adaptations (Mason & Donovan, 2015), root traits (Geng et al., 2014) and leaf anatomy (Bucher et al., 2016).

CHAPTER 5

ARE REPRODUCTIVE TRAITS IN PLANTS ASSOCIATED WITH THE LEAF

ECONOMIC SPECTRUM?

5.1 Introduction

Several important leaf traits covary universally (Díaz et al., 2015; Heberling & Fridley, 2012; Wright et al., 2004). The leaf economic spectrum represents a single axis of variation that describes multivariate covariations between leaf traits (Wright et al., 2004). One end of the spectrum contains plants following a 'fast' life history strategy (photosynthetically highly active, short-lived leaves with high nutrient content and low leaf mass per unit area (LMA)). The other end of spectrum contains plants following a 'slow' life history strategy (slower photosynthetic rate, lower nutrient content long-lived leaves and higher LMA).

The leaf economics spectrum has recently been expanded to include other plant traits including plant height, wood density and decomposition rate, as well as the morphology of stems and roots (Poorter et al., 2014; Falster et al., 2011; Cornelissen et al., 2003; Westoby et al., 2002). Recent studies also suggested that leaf traits could be good predictors of overall plant performance (Díaz et al., 2015; Poorter & Bongers, 2006), i.e. the continuum of slow-growing to fast-growing species at the leaf level might apply to whole plant performance.

The slow to fast life history continuum could also extend to encompass reproductive traits. Plants with a 'fast' life history traits acquire resources at a faster pace and could therefore reproduce more rapidly. For example, plants with fast leaf turnover times may also have faster turnover rates of reproductive parts such as flowers and fruits (Reich, 2014; Méndez-Alonzo et al., 2012; Burns & Lake, 2009; Santiago, 2007).

Here, I attempt to establish relationships between leaf traits and vegetative phenologies of 12 woody plant species from a temperate rainforest in New Zealand to flower and fruit traits and their reproductive phenologies. More specifically, I predict that plants with short leaf lifespans, low LMA and short leaf development times invest less in flowers and seeds and have shorter reproductive phenologies. On the other hand, plants with longer leaf life spans, higher LMA and longer leaf longevities have to invest more in flowers and seeds and have more prolonged reproductive phenologies.

5.2 Methods

Phenological traits

Leaf longevity and leaf development times were quantified by marking five leaf buds on 10 individuals of 12 common tree species in ZEALANDIA (Section 2.1 and Section 4.2, Table 5.1). The longevities and development times of fruits and flowers were quantified by observing the canopies of 10 marked trees from each species for leaf observations as described in Section 2.1. Flower development time were quantified for each tree as the time interval between the first observation of flower buds and the first observation of open flowers. Flower development times were then averaged among the 10 marked individuals for each species. Flower longevities were quantified similarly as the time interval between the first observation of open flowers and when all flowers were abscised. Fruit development times were quantified as the time interval between flower anthesis and the presence of mature fruits. Finally, fruit longevities were quantified for each species as the average number days ripe fruits occurred on each marked tree.

Morphological traits

Leaf mass per unit area (LMA) measurements were done following the protocols for measurement of plant functional traits (Pérez-Harguindeguy et al., 2013; Cornelissen et al., 2003). Fully expanded leaves with petioles from adult plants (50 leaves per species) were collected. Leaf area for fresh leaves was measured using a Li-Cor 3100 leaf area meter (Li-Cor, Lincoln, Neb) and dried for 48 h at 65° C for determination of dry mass. LMA (mass/area, gm/m^2) was calculated for each leaf and averaged for each species.

Flower sizes were quantified by obtaining flower diameter, flower length and the length of the flower pedicel from the Flora of New Zealand (Allan, 1982). Principle Components Analysis was then used to extract a single axis representing flower size.

Seed sizes were quantified by obtaining average seed length and seed width from the New Zealand Seed Atlas (Webb & Simpson, 2001). Seed lengths were then multiplied by seed widths to obtain a single seed size estimate for each species.

To assess whether leaf traits were associated with flower and fruit traits, Principle Components Analysis was used to extract a single axis representing leaf development times, LMA and leaf longevity. The first principal component was then compared to reproductive traits using Pearson's Correlation. Log transformations were applied whenever necessary to meet the assumptions of inferential statistics.

All calculations and analyses were carried out using R v.3.0.2 (R Team, 2013).

5.3 Results

Leaf traits varied widely among study species (Table 5.1). Leaf development times ranged from 45 to 120 days ($\bar{x}$ = 92, σ^2 = 31.56), leaf longevities ranged from 6 to 36 months ($\bar{x}$ = 608, σ^2 = 240.54) and leaf mass per unit area (gm/m^2) ranged from 0.38 to 1.46 g ($\bar{x}$ = 0.74, σ^2 = 0.35). All three leaf traits were positively correlated (Figure 5.1). Leaf mass per unit area increased with leaf development time (r = 0.70, p < 0.05) and leaf longevity (r = 0.82, p < 0.01). Leaf development times also increased with leaf longevity (r = 0.81, p < 0.01). Given the strong degree of covariance among leaf trait data, the first principal component recovered a high degree of variation (85.11%) among variables (factor loadings were 0.567, 0.569, and 5.95 for leaf development time, leaf mass per unit area and leaf longevity, respectively) (Table 5.2).

Flower buds took between 45 to 120 days to develop into open flowers ($\bar{x}$ = 75.25, σ^2 = 22.82) and remained on parent plants for 45 to 60 days ($\bar{x}$ = 54.83, σ^2 = 8.24). Flower development times were unrelated to the principal component representing leaf traits (Figure 5.2, r = 0.41, p > 0.05). Additionally, there was no relationship between leaf traits and flower longevities (Figure 5.2, r = -0.08, p > 0.05). Overall flower size estimates derived from the first principal component, which explained 62.68% among three flower variables (factor loadings were 0.58, 0.68, 0.45 for flower length, flower diameter and pedicel length, respectively), was also unrelated to the first principal component representing leaf traits (Figure 5.2, r = -0.15, p > 0.05).

Table 5.1: Study species with their respective average (± 1 SD) leaf development time

(LDT, days), leaf mass per unit area (LMA, gm/m^2) and leaf longevity (days).

Species	LDT	LMA	Leaf longevity
Fuchsia excorticata	45 (±11.82)	38.24 (±8.49)	210 (±24.30)
Geniostoma rupestre	50 (±9.14)	39.01 (±2.91)	423 (±36.00)
Macropiper excelsum	60 (±5.45)	40.08 (±3.97)	450 (±18.90)
Schefflera digitata	90 (±14.02)	54.78 (±20.31)	540 (±21.00)
Aristotelia serrata	90 (±12.22)	61.46 (±10.29)	510 (±38.10)
Coprosma grandifolia	90 (±10.33)	73.87 (±13.70)	540 (±45.00)
Melicytus ramiflorus	87 (±15.58)	76.71 (±7.48)	555 (±53.70)
Hedycarya arborea	150 (±12.36)	80.24 (±24.45)	840 (±28.80)
Coprosma robusta	110 (±16.33)	96.67 (±10.37)	860 (±36.00)
Myoporum laetum	90 (±10.20)	99.46 (±11.81)	864 (±25.20)
Pittosporum eugenioides	100 (±9.50)	101.05 (±18.38)	867 (±28.90)
Pseudopanax arboreus	120 (±15.90)	146.16 (±11.36)	900 (±39.00)

Table 5.2: Factor loadings of three leaf trait variables on the first principal component and variance explained by the respective components.

Variable	PC1
Leaf development time	0.567
LMA	0.569
Leaf longevity	0.595
Variance explained	85.11%
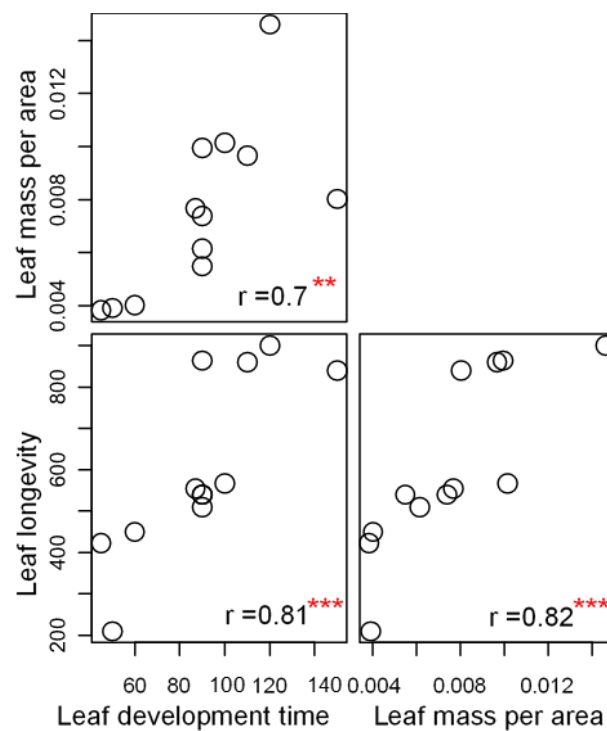
Figure 5.1 Correlations matrix among leaf development time (days), LMA (gm/cm^2) and leaf longevity (days). The "r" values represent Pearson's correlation coefficients, * $p<0.05$, ** $p<0.01$, *** $p<0.001$.
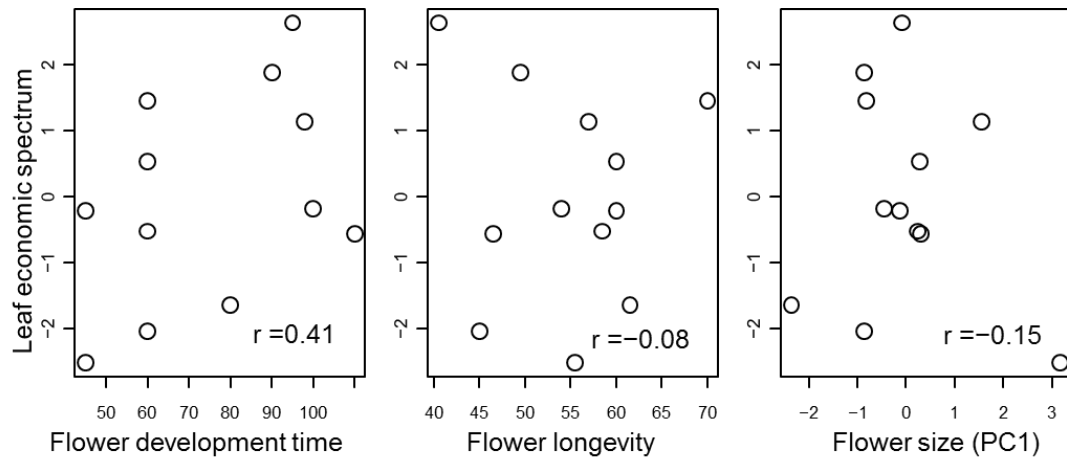
Figure 5.2: Relationships between the leaf economic spectrum and flower traits. The y-axis represents the first principal component of interspecific values of leaf development times, LMA and leaf longevities. Flower development times and longevities were measured in days and flower sizes in mm. Flower length, diameter and pedicel length values all measured in mm, were log transformed to meet the assumptions of inferential statistics and subjected to principal component analysis to achieve a single axis comparison with leaf traits.

After flower petals fall off an open flower, it took 3 to 12 months for development into a ripe fruit ($\bar{x}$=177.08, σ^2=88.61) and ripe fruits were available from 45 to 150 days ($\bar{x}$=72.91, σ^2=33.40). The first principal axis representing leaf traits showed significantly high correlations with each fruit trait (Figure 5.3). Specifically, the development time of fruits was highly correlated with leaf traits (r=0.72, p<0.001). Leaf traits were also

significantly correlated with fruit longevity (r=0.59, p<0.01) and fruit size ($\bar{x}$=12.57, σ^2=19.82) (r=0.66, p<0.01).

s
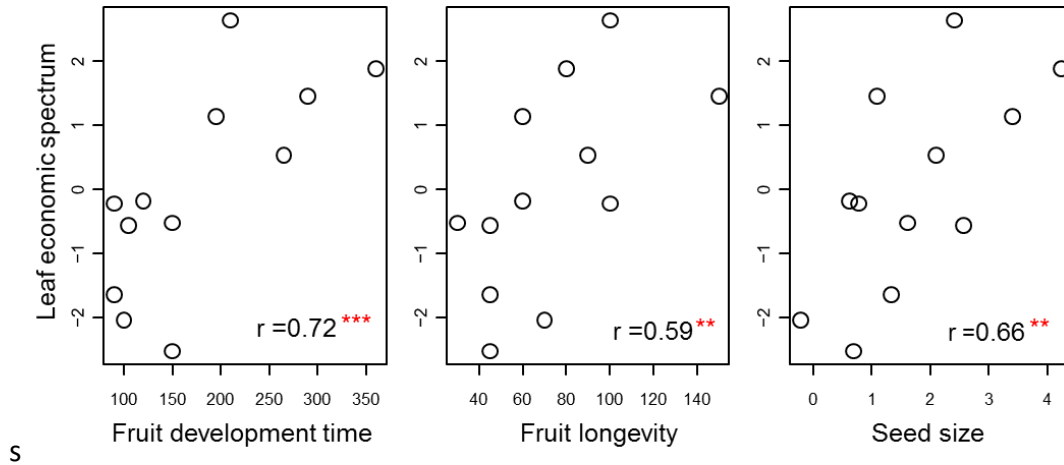
Figure 5.3: Relationships between the leaf economic spectrum and fruit traits. The y axis is generated by the principal component analysis of interspecific values of leaf development time, LMA and leaf longevity. Fruit development time and longevity were measured in days and seed sizes in mm^2. Seed size values were log transformed to meet the assumptions of inferential statistics.

5.4 Discussion

Leaf traits in the 12 tree species studied covaried according to the leaf economics spectrum. Although leaf traits were not associated with flower traits, they were associated with fruit traits. Species with slowly developing, long-lived leaves with high LMA produced slowly developing, long-lived fruit that contained large seeds. Therefore,

the 'fast-to-slow' continuum of leaf traits in my study species also encompasses fruit and seed traits.

Leaf trait relationships in this study are consistent with the leaf trait relationships reported elsewhere (Niinemets, 2015; Sack et al., 2013; Wright & Sutton-Grier, 2012; Blonder et al., 2011; LS & Antiago, 2007; Wright et al., 2005). Although my study did not encompass the full spectrum of leaf traits considered previously, recent studies have shown that LMA often reflects a significant amount of variation in other plants traits statistically (e.g. growth rates, Poorter et al., 2014). Strong correlations between leaf development times, leaf longevities and LMA suggest that thick, tough leaves take longer to develop and persist for longer on parent plants.

Leaf traits were unrelated to flower traits, suggesting that 'fast' versus 'slow' leaf trait co-variation does not extend to encompass flowers. The phenology and energetic investment in flowers can be influenced by numerous factors such as the type of pollinators, the quality and quantity of nectar, and the fragrance, color and size of flowers (Reekie & Bazzaz, 2011; Bazzaz et al., 1987). Flowers are designed to attract pollinators, either specialists or generalists (Laverty & Plowright, 1988), and biomass investment must be made accordingly. The arrival of a pollinator for a successful pollination can be altered by factors of the environment, such as changes in wind speed in wind-pollinated species and competition for a pollinator in animal pollinated species. A flower's eventual function is seed setting from pollination and the flower's longevity is restricted by pollinator visitation. Hence, the strategy of investment is likely to differ between leaves and flowers. Several resource allocation theories argue that the energy

spent on one function is mutually exclusive to other competing functions (Obeso, 2002; Bazzaz et al., 2000; de Jong, 1993). Further research on flower traits accounting for different attributes of flower and pollinator types might provide a clearer picture of the plant's strategy for carbon investment in its flowers.

Unlike flowers, fruit traits co-varied with leaf traits. Plants with long lived and higher LMA leaves produce fruits that take a longer time to develop, stay on the parent plant for a longer time as well as having larger seed size. The species studied here were fleshy fruited which are shown to bear heavier seeds (Bolmgren & Eriksson, 2010). This has been linked to evolution of specialist frugivores that provide longer dispersability for these seeds (Bolmgren & Eriksson, 2010; Wotton, 2007; Lord, 2004; Jordano, 1995) but there is little evidence of frugivores contributing to fruit trait evolution (Herrera, 2002; Levey & Benkman, 1999). Also, larger seeds are known to be stronger competitors during seedling establishment (Henery & Westoby, 2001; Jakobsson & Eriksson, 2000).

The number of seeds, their size, their mass and the seed bank involve tradeoffs for selecting one or the other (Henery & Westoby, 2001; Leishman & Westoby, 2000; Thompson, Band, & Hodgson, 1993). Small-seeded species are associated with higher numbers of seeds. Some evidence of seed mass co-varying with leaf traits come from the "leaf-height-seed" plant strategy theory (Laughlin et al., 2010; Burns & Lake, 2009; Westoby, 1998). Reich et al. (1998) found an inverse relationship of relative growth rate with seed mass as well as leaf lifespan among nine boreal tree species. The positive co-variance between development time of leaves and fruits in this study also suggests a slower growth rate for plants with bigger seed sizes and longer leaf lifespans. Inclusion

of other fruit attributes such as fruit mass, fruit volume and seed weight in future research might add more to our understanding of carbon investment strategies of plants in their vegetative and reproductive organs. Regardless of the adaptive mechanism underpinning relationships between fruit and leaf traits, the fast versus slow continuum can be extended to encompass fruit and seed traits in these species.

In the context of global trait research progressing towards whole plant economics, this study provides evidence of systematic co-variance between leaf and fruit traits and emphasizes the need for extending research to include reproductive traits in the global trait database. The inclusion of phenology provided a better understanding of the time allocation by plants in each phase of their life and added to our understanding of resource allocation. Though flower traits did not support my predictions, I emphasize the need to include a wider reproduction trait suite in future research.

CHAPTER 6

GENERAL DISCUSSION

6.1 Thesis Summary

This thesis discusses seasonality, phenological patterns and plant trait correlations in a New Zealand forest. Understanding the ecological processes involves identifying as well as quantifying ecological patterns in the plant community (Fortin & Dale 2005). Phenological observations on the timing of major life cycle events of plants - flowering, fruiting, leaf production and leaf abscission - were compiled to document patterns of seasonality in Chapter 3. Important findings include distinct seasonality in all four phenological events, consistency of seasons between two successive years of study and timing of phenological events in response to climatic conditions from the onset of spring to the end of autumn with a period of inactivity in winter. As discussed in Chapter 3, while only a small sample of common plant species from a regenerating New Zealand native forest are studied, the results provide baseline information for wider phenological study in New Zealand.

In Chapter 4, I explored differences in leaf longevities and their seasonality in production and abscission. Although there were distinct leaf production and abscission seasons, leaves produced at the same time of year may abscise after different time intervals determined by their longevities. However, leaf longevities tended to be categorical rather than continuous and they maintained their seasonality in abscission times. Species mainly abscise their leaves either after 6-7 months, 15-18 months or 27-30 months. *Pseudopanax aboreus* still had not abscised some marked leaves at the end of the 30th month which indicated a possible leaf longevity of more than 3 years. Further, in spite of all the differences in longevities, the marked leaves were abscised

between February and May each year coinciding with the leaf abscission seasons described in Chapter 3. Although there has been much interest in leaf trait research in the past decade, leaf longevity remains lesser known than other plant traits. The results not only shed light on patterns of leaf longevity but also pioneer an area for further research on seasonality in leaf longevity.

Chapter 5 discusses the relationship between leaf, flower and fruit traits and their relation to the leaf economic spectrum. The leaf economic spectrum (LES) describes multivariate correlations between a combinations of key leaf traits which vary along a principal axis that aided in understanding the strategies of plants associated with the terrestrial carbon cycle. This chapter tested connections between leaf phenological and morphological traits against their analogous reproductive traits. Firstly, in addition to the leaf longevity and LMA, the development times of leaves conformed to the patterns of leaf economic spectrum. Secondly, the fruit development time, longevity and seed size were also related to the leaf economic spectrum. However, flower traits did not show any significant correlation with leaf traits. The inclusion of phenology in plant trait research gives a better understanding of time allocation by plants in each phase of their life and of the tradeoffs between costs and benefits of allocation.

6.2 Implications of research

Conservation planning

Understanding ecological interactions and the patterns generated by underlying processes are important in conservation planning for successful and sustainable establishment of endangered flora and fauna (Myers et al., 2000). For example, phenological studies can provide indications of possible biological interactions between species in a community as such as competition for food resources or food abundance, and also are useful for assessing the effect of naturalised plants and introduced animals on the community ecology of native plants and animals. The New Zealand forest ecosystem and its biota have been recovering from large-scale forest clearance since the 1800s as well as from the introduction of invasive mammals such as brushtail possums (*Trichosurus vulpecula*) and rats (*Rattus spp.*) (Fitzgerald, 1976; O'Donnell & Dilks, 1994). The results of phenological studies have been used to assess pest control methods along with ensuring food availability for reintroduced native species (Cummings et al., 2014; Armstrong et al., 2002; Perrott & Armstrong, 2000; Allen, Fitzgerald, & Efford, 1997; O'Donnell & Dilks, 1994; Fitzgerald, 1976). Community scale studies in phenology, such as the present one, also broaden our understanding of the patterns of forest productivity and of reproduction patterns in New Zealand plants.

Phenological monitoring and Climate change research

This study and intended publications contribute to understanding reproductive as well as vegetative phenologies in some common plant species in New Zealand forests. More widely, however, the data resource obtained from phenological monitoring will be a potential resource for ecologists and plant scientists, and potentially of applied benefit to the wider public such as to agriculture and horticulture. Phenology affects the diversity, distribution and abundance of species, ecosystem services, food webs, and the global cycles of water and carbon, so has many wider impacts (Encinas-Viso, Revilla, & Etienne, 2012; Beaubien & Hamann, 2011; Lieth, 1974). Due to global warming, shifts in phenological timings in plants have been evident in the last decade (Tooke & Battey, 2010; Walther et al., 2002; Kramer, Leinonen, & Loustau, 2000). However, the responses to climate change can be different in different species and communities. Monitoring of phenology aids in tracking trends of important recurring phenological events. There are numerous networks around the world which record and share the phenological information on the World Wide Web (for example, the European Phenology Network, US National Phenology Network, UK Phenology Network). A primary motive for recording phenological events through these networks is to assist climate change research and policy development and decision making by creating a long term, standardized database. Climate change has altered lifecycles of insects and pathogens, caused shifts in phenology, resulting in phenological and ecological mismatch in some migratory species. The Integrative Panel on Climate Change (IPCC) states phenology as "the simplest process in which to track changes in the ecology of species in response to climate change" (IPCC 2013).

A global plant trait database initiative called TRY is a data repository which contains plant traits such as morphological, physiological or phenological features measured at the individual level, contributed to electronically from around the world (Kattge et al., 2011). The main objectives of the repository are to promote a trait based approach through a web-archive so as to understand the emergences and consequences of evolutionary and community ecology. This study has tested several new traits in the context of global trait research and has shown them to conform to the concept of the leaf economic spectrum. The scientific publications from this thesis will add a new trait dataset to the repository.

6.3 Future directions

The understanding of how plant species differ or comply in the timing of life-cycle events and how the morphological and functional traits vary between plant species has increased markedly in recent years (Díaz et al., 2015; Poorter, Lambers, & Evans, 2014; Kikuzawa & Lechowicz, 2011; Wright et al., 2004). In this regard, I discuss some areas that still need more attention and research that needs to be considered in order to fill gaps, as well as to further our understanding of phenological patterns, seasonality and plant trait correlations.

1. This thesis presents a community level phenological study which included 12 common plant species in New Zealand forests. Further exploration of the

seasonality and phenological patterns for more species and for longer duration will obviously enrich our understanding of the New Zealand forest ecosystem.

2. Leaf longevity and LMA are shown to be related and chapter 3 suggested a strong influence of seasonality on leaf longevity. Even though leaf longevity is included widely in trait research, the data resource for leaf longevity is scarce. Also, quantifying the individual influence of LMA and climate on resultant leaf longevity is desirable in order to better understand the strong seasonality displayed by forest plants in this thesis.

3. The fast-slow continuum plant traits postulated in the leaf economic spectrum is increasingly being related to other plant traits and is believed to comply with whole plant characteristics, but reproductive traits were not included in the traits correlation research. Results in this study show a strong correlation between leaf and fruit traits. This study only included phenological intervals and flower size and seed size as reproductive traits. The addition of other morphological traits such as flower mass, fruit mass, and nectar content may influence resultant correlations. Future research to include comprehensive sets of leaf, flower and fruit traits may shed more light on the resultant trait relationships.

6.4 Conclusions

Here, I have presented a community scale phenological study, the patterns of lifehistory events within the community and demonstrated trait correlations between leaves, flowers and fruits. My main conclusions are:

- There are distinct and consistent phenological seasons in New Zealand forests, flowering starting with the onset of spring closely followed by leaf production. While fruiting peaks about three months after peak leaf production, by the end of autumn trees abscise their old leaves before the onset of winter.

- Leaf longevity and LMA differed widely between 12 study species. Leaf longevity varied from 6 to 30 months with the possibility of greater longevity for one of the species. Interestingly the longevities clustered around a regular interval of 12 months coinciding with leaf abscission seasons displayed in chapter 2. Regardless of the length of the life-time, leaves were abscised largely between February and May. Hence, leaf longevity is influenced by seasonality in climate along with leaf construction costs (LMA).

- Plants with leaves that have higher LMA and longevity are likely to have fruits that take a longer time to develop, stay longer on plants and have a larger seed size, in contrast to plants with fast growth traits. This thesis is evidently one of the first attempts to relate the leaf economic spectrum to reproduction in plants and opens up possibilities of further exploration of this remarkable relationship.

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APPENDICES

1. **CIRCULAR STATISTICS R SCRIPT (Adapted from Ting et al. 2008)**

```
library(CircStats)

library(circular)
```

 # Changing degrees to radians

```
Deg2Rad = function(values.in.deg) {values.in.deg*pi/180}

Rad2Deg = function(values.in.rad) {values.in.rad*180/pi}
```

 # Calculate the angular mean (Zar 1996) Chapter 24.4

```
circ.stats = function(counts.v, ...) {

 bins   <- length(counts.v)                    # number of equal sized segments

 lambda  <- 2*pi/bins                          # size of one segment in radians

 angles  <- 360/(2*bins) + (0:(bins-1))*360/bins     # angles at sector mid-points

 angles  <- Deg2Rad(angles)

 n <- sum(counts.v)                            # n = Number of observation events

 average <- n/bins

 ifelse (n==0, X <- 0, X <- sum(counts.v*cos(angles))/n)

 ifelse (n==0, Y <- 0, Y <- sum(counts.v*sin(angles))/n)

 r.length  <- sqrt(X^2 + Y^2)                    # mean vector length for point data

 rc.length <- r.length*((lambda/2)/sin(lambda/2))      # correction for grouped data

 if (X>0)  r.angle <- atan(Y/X)

 if (X<0)  r.angle <- atan(Y/X) + pi

 if (X==0) r.angle <- NA

 ifelse (r.angle<0, r.angle <- r.angle + (2*pi), NA)      # convert negative angles to positive

 circSD <- 180/pi*sqrt(-2*log(r.length))              # calculate the angular dispersion

 circSDc <- 180/pi*sqrt(-2*log(rc.length))

 output.v <- c(r.length, rc.length, r.angle, Rad2Deg(r.angle), circSD, circSDc, bins, average)

 dim(output.v) <- c(1,8)

 colnames(output.v) <- c("r.length", "rc.length", "r.angle.rad", "r.angle.deg", "circSD",
"circSDc", "bins", "average")

 output.v

}
```

rose-diagram with cross hairs

```
circular.hist4 = function (counts.v, resln = 360, limit = max(counts.v), type = linear, ...) {
  bins <- length(counts.v)
  angles <- (0:bins)*(2*pi/bins)
  plot.new ()
  plot.window (xlim = c(-limit, limit), ylim = c(-limit, limit), asp = 1, ...)
  #plot (0, 0, xlim = plot.limits, ylim = plot.limits, xaxt = "n", yaxt="n", ...)
  # plot (0, 0, xaxt = "n", yaxt="n", ...)
  #axis (1, at = 0); axis (2, at = 0)
  for (i in 1:bins) {
    draw.seg (r = counts.v [i], theta1 = angles [i], theta2 = angles [i+1], resln = resln, ...)
  }
}
```

add a circle of labels, e.g. use with circular.hist4

```
circular.labels = function (labels.v, r=0.5, cex = 0.8, txtcol = NA, ...) {
  bins <- length(labels.v)
  angles <- 360/(2*bins) + (0:(bins-1))*360/bins
  angles <- Deg2Rad(angles)
  for (i in 1:bins) text(r*sin(angles[i]), r*cos(angles[i]), labels.v[i], cex=cex, col=txtcol, ...)
}
```

add axes to circular.hist4

```
draw.crosshairs = function(x = 0, y = 0, xmax = 1, xmin = -xmax, ymax = xmax, ymin = xmin,
               tic.interval = round(floor(xmax-xmin)/4), tic.size = tic.interval/20,
               tic.labels = TRUE, spacer = 2, axis.labels = c("0", "90", "180", "270"), ...) {
  lines (c(x, x), c(ymin, ymax), ...)
  lines (c(xmin, xmax), c(y, y), ...)
  if (tic.interval == 0) { tic.interval <- signif((xmax - xmin)/4, 1) }
  tic.pos <- x
  while (tic.pos < ymax) {
```

```
    tic.pos <- tic.pos + tic.interval

    lines (c(x-tic.size, x+tic.size), c(tic.pos, tic.pos), ...)

    if (tic.labels == TRUE) text(x-(spacer*tic.size), tic.pos, tic.pos, adj = c(1,0.5), ...)

   }

  tic.pos <- x

  while (tic.pos > ymin) {

    tic.pos <- tic.pos - tic.interval

    lines (c(x-tic.size, x+tic.size), c(tic.pos, tic.pos), ...)

    if (tic.labels == TRUE) text(x-(spacer*tic.size), tic.pos, tic.pos, adj = c(1,0.5), ...)

   }

  tic.pos <- y

  while (tic.pos < xmax) {

    tic.pos <- tic.pos + tic.interval

    lines (c(tic.pos, tic.pos), c(y-tic.size, y+tic.size), ...)

    if (tic.labels == TRUE) text(tic.pos, y-(spacer*tic.size), tic.pos, adj = c(0.5,1),...)

   }

  tic.pos <- y

  while (tic.pos > xmin) {

    tic.pos <- tic.pos - tic.interval

    lines (c(tic.pos, tic.pos), c(y-tic.size, y+tic.size), ...)

    if (tic.labels == TRUE) text(tic.pos, y-(spacer*tic.size), tic.pos, adj = c(0.5,1),...)

   }

}


# Changing groups to points for monthly binned data


groups2points = function(counts.v, factor = 1, pointplot = TRUE, ...) {

  bins <- length(counts.v)              # number of bins in the grouped data

  angles <- (0:bins)*(2*pi/bins)        # angles of sector edges (start = 0 = end = 360)

  points.on.circ <- c()

  pos <- 1
```

```
  for (i in 1:bins) {

   theta1 <- angles[i]

   theta2 <- angles[i+1]

   if ((counts.v[i] * factor) > 0) {

    incrmt <- (2*pi) / (bins * round(counts.v[i] * factor))

    points.on.circ <- c(points.on.circ, seq(theta1+(incrmt/2), to = theta2-(incrmt/2), by =
incrmt))

    theta3 <- points.on.circ[pos]

    pos <- pos + round(counts.v[i] * factor)

   }

  }

  if (pointplot == TRUE) { point.plot(points.on.circ, ...) }

  points.on.circ

}
```

Examples

```
#month labels

labels.v  <- c("J", "F", "M", "A", "M", "J", "J", "A", "S", "O", "N", "D")

#No. of species flowering each month Year 1

test.counts.flY1 <- c(3, 2, 0, 0, 0, 0, 0, 1, 2, 4, 5, 4)

#No. of species flowering each month Year 2

test.counts.flY2 <- c(2, 1, 0, 0, 0, 0, 0, 0, 2, 2, 5, 4)

#Calculating mean angle

circ.stats (test.counts.flY1)
```

#Rayleigh's test of uniformity and Watson U^2 test

```
data1 <- groups2points (test.counts.flY1)   #converting grouped data to continuous

rayleigh.test(data1)

data2 <- groups2points (test.counts.flY2)

watson.two.test (data1, data2)
```

#Plotting Circular rose plot with monthly labels axes labels

```
circular.hist4 (test.counts.fl1, col = "pink", xlab ="", ylab = "Flowers")

circular.labels (labels.v, r = max(test.counts.fl1)*0.3)

draw.crosshairs (xmax = max(test.counts.fl1))
```

2. Number of species displaying each phenological stage through the year using in Chapter 2.

Phenology	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2012												
Flowering	3	2	0	0	0	0	0	1	2	4	5	4
Fruiting	4	5	4	3	1	0	0	0	0	1	2	2
Leaf production	5	0	0	0	0	0	0	0	0	4	7	9
Leaf abscission	0	3	6	8	6	0	0	0	0	0	0	0
2013												
Flowering	2	1	0	0	0	0	0	0	2	2	5	4
Fruiting	3	3	3	3	1	0	0	0	0	1	1	2
Leaf production	4	1	0	0	0	0	0	0	0	6	8	7
Leaf abscission	0	3	7	7	6	0	0	0	0	0	0	0

3. Source table for Figure 6 on Chapter 3 (leaf traits relationship between leaf longevity and mean Leaf mass area (LMA))

LMA (gm/cm2)	Leaf Longevity (months)	Code for fig. 6 & 7
0.003824	14.1	2
0.003901	7	1
0.004008	15	3
0.005478	18	4
0.006146	17	5
0.007387	18	6
0.007671	18.5	7
0.008024	28	8
0.009667	28	9
0.009946	28.8	10
0.01015	28.9	11
0.014616	30	12

4. Source table for Figure 7 on Chapter 3 (Patterns of leaf longevity in 12 study species)

Species	Months	Phenophase	Leaves	sps
Fuchsia excorticata	0.5	Production	1	1
Fuchsia excorticata	1	Production	3	1
Fuchsia excorticata	1.5	Production	6	1
Fuchsia excorticata	2	Production	9	1
Fuchsia excorticata	2.5	Production	13	1
Fuchsia excorticata	3	Production	18	1
Fuchsia excorticata	6	Abscission	2	1
Fuchsia excorticata	6.5	Abscission	5	1
Fuchsia excorticata	7	Abscission	11	1
Fuchsia excorticata	7.5	Abscission	20	1
Fuchsia excorticata	8	Abscission	10	1
Fuchsia excorticata	8.5	Abscission	2	1
Macropiper excelsum	2	Production	2	3
Macropiper excelsum	2.5	Production	3	3
Macropiper excelsum	3	Production	5	3
Macropiper excelsum	3.5	Production	10	3
Macropiper excelsum	4	Production	20	3
Macropiper excelsum	4.5	Production	10	3
Macropiper excelsum	18.5	Abscission	1	3
Macropiper excelsum	19	Abscission	10	3
Macropiper excelsum	19.5	Abscission	19	3
Macropiper excelsum	20	Abscission	20	3
Schefflera digitata	3	Production	5	4
Schefflera digitata	3.5	Production	8	4
Schefflera digitata	4	Production	15	4
Schefflera digitata	4.5	Production	20	4
Schefflera digitata	5	Production	2	4
Schefflera digitata	19	Abscission	1	4
Schefflera digitata	19.5	Abscission	4	4
Schefflera digitata	20	Abscission	10	4
Schefflera digitata	20.5	Abscission	19	4
Schefflera digitata	21	Abscission	16	4
Aristotelia serrata	2	Production	3	5
Aristotelia serrata	2.5	Production	10	5
Aristotelia serrata	3	Production	17	5
Aristotelia serrata	3.5	Production	15	5
Aristotelia serrata	4	Production	5	5
Aristotelia serrata	12	Abscission	2	5
Aristotelia serrata	12.5	Abscission	1	5
Aristotelia serrata	18.5	Abscission	9	5
Aristotelia serrata	19	Abscission	15	5

Aristotelia serrata	19.5	Abscission	25	5
Aristotelia serrata	20	Abscission	10	5
Melicytus ramiflorus	3	Production	3	7
Melicytus ramiflorus	3.5	Production	5	7
Melicytus ramiflorus	4	Production	17	7
Melicytus ramiflorus	4.5	Production	20	7
Melicytus ramiflorus	5	Production	5	7
Hedycarya arborea	3	Production	10	8
Hedycarya arborea	3.5	Production	13	8
Hedycarya arborea	4	Production	22	8
Hedycarya arborea	4.5	Production	5	8
Hedycarya arborea	23.5	Abscission	3	8
Hedycarya arborea	31	Abscission	10	8
Hedycarya arborea	31.5	Abscission	11	8
Hedycarya arborea	32	Abscission	20	8
Hedycarya arborea	32.5	Abscission	5	8
Hedycarya arborea	33	Abscission	1	8
Myoporum laetum	3	Production	16	10
Myoporum laetum	3.5	Production	20	10
Myoporum laetum	4	Production	14	10
Myoporum laetum	21.5	Abscission	3	10
Myoporum laetum	22	Abscission	2	10
Myoporum laetum	22.5	Abscission	2	10
Myoporum laetum	30.5	Abscission	5	10
Myoporum laetum	31	Abscission	13	10
Myoporum laetum	31.5	Abscission	15	10
Myoporum laetum	32	Abscission	18	10
Myoporum laetum	32.5	Abscission	2	10
Pseudopanax arboreus	3	Production	8	12
Pseudopanax arboreus	3.5	Production	10	12
Pseudopanax arboreus	4	Production	20	12
Pseudopanax arboreus	4.5	Production	12	12
Pseudopanax arboreus	22.5	Abscission	1	12
Pseudopanax arboreus	23	Abscission	1	12
Pseudopanax arboreus	32	Abscission	6	12
Pseudopanax arboreus	32.5	Abscission	10	12
Pseudopanax arboreus	33	Abscission	5	12
Pseudopanax arboreus	33.5	Abscission	1	12
Geniostoma rupestre	0.5	Production	5	2
Geniostoma rupestre	1	Production	15	2
Geniostoma rupestre	1.5	Production	20	2
Geniostoma rupestre	2	Production	10	2
Geniostoma rupestre	15	Abscission	3	2
Geniostoma rupestre	15.5	Abscission	10	2

Geniostoma rupestre	16	Abscission	17	2
Geniostoma rupestre	16.5	Abscission	13	2
Geniostoma rupestre	17	Abscission	7	2
Geniostoma rupestre	17.5	Abscission	0	2
Geniostoma rupestre	18	Abscission	0	2
Pittosporum eugenioides	2.5	Production	4	11
Pittosporum eugenioides	3	Production	10	11
Pittosporum eugenioides	3.5	Production	16	11
Pittosporum eugenioides	4	Production	14	11
Pittosporum eugenioides	4.5	Production	6	11
Pittosporum eugenioides	30	Abscission	5	11
Pittosporum eugenioides	30.5	Abscission	10	11
Pittosporum eugenioides	31	Abscission	20	11
Pittosporum eugenioides	31.5	Abscission	15	11
Coprosma robusta	2	Production	0	9
Coprosma robusta	2.5	Production	5	9
Coprosma robusta	3	Production	10	9
Coprosma robusta	3.5	Production	15	9
Coprosma robusta	4	Production	12	9
Coprosma robusta	4.5	Production	8	9
Coprosma robusta	18	Abscission	7	9
Coprosma robusta	30	Abscission	10	9
Coprosma robusta	30.5	Abscission	15	9
Coprosma robusta	31	Abscission	18	9
Coprosma grandifolia	3	Production	5	6
Coprosma grandifolia	3.5	Production	15	6
Coprosma grandifolia	4	Production	20	6
Coprosma grandifolia	4.5	Production	10	6
Coprosma grandifolia	18.5	Abscission	1	6
Coprosma grandifolia	19	Abscission	10	6
Coprosma grandifolia	19.5	Abscission	19	6
Coprosma grandifolia	20	Abscission	20	6

5. Source table for figure 8 on Chapter 3 (phenological patterns of leaves for two years)

Month	Seasons	Months	Leaf Phenology
September	Spring	1	0
	Spring	1.5	0
October	Spring	2	0
	Spring	2.5	0
November	Spring	3	0
	Spring	3.5	3
December	Summer	4	5
	Summer	4.5	3
January	Summer	5	1
	Summer	5.5	0
February	Summer	6	0
	Summer	6.5	0
March	Autumn	7	0
	Autumn	7.5	0
April	Autumn	8	-3
	Autumn	8.5	-4
May	Autumn	9	-3
	Autumn	9.5	-2
June	Winter	10	0
	Winter	10.5	0
July	Winter	11	0
	Winter	11.5	0
August	Winter	12	0
	Winter	12.5	0
September	Spring	13	0
	Spring	13.5	0
October	Spring	14	0
	Spring	14.5	1
November	Spring	15	2
	Spring	15.5	4
December	Summer	16	3
	Summer	16.5	2
January	Summer	17	0
	Summer	17.5	0
February	Summer	18	0
	Summer	18.5	0
March	Autumn	19	0
	Autumn	19.5	0
April	Autumn	20	-1
	Autumn	20.5	-2
May	Autumn	21	-4

	Autumn	21.5	-3
June	Winter	22	-2
	Winter	22.5	0
July	Winter	23	0
	Winter	23.5	0
August	Winter	24	0
	Winter	24.5	0
September	Spring	25	0
	Spring	25.5	0
October	Spring	26	0
	Spring	26.5	0
November	Spring	27	1
	Spring	27.5	2
December	Summer	28	5
	Summer	28.5	3
January	Summer	29	1
	Summer	29.5	0
February	Summer	30	0
	Summer	30.5	0

6. **Source table flower size (PC1) in figure 10 on Chapter 4**

Flower length	Flower diameter	Pedicel length
4	3	5.5
37	30.2	13
1	2.5	2
10	7	3.2
8	5	8
16.6	5.5	1
5	3.5	7
4	6	1.2
15	4	0.5
9.4	15	11
5.2	9.5	3.9
4.7	7.1	3.8

7. Source table for figure 10, 11 and 12. Phenological variables were measured in days, LMA in g/m2, flower and seed size components in cm on Chapter 4.

Sps	Leaf development time	LMA	Leaf longevity	Flower development time	Flower longevity	Fruit development time	Fruit longevity	Flower size (PC1)	Seed size
Gr	45	38.24165	423	60	45	100	70	3	0.8
Fe	50	39.01431	210	45	55.5	150	45	15	2
Me	60	40.07969	450	80	61.5	90	45	5	3.8
Sd	90	54.78255	540	110	46.5	105	45	7	12.99
As	90	61.46416	510	60	58.5	150	30	5	5
Cg	90	73.87235	540	45	60	90	100	6	2.18
Mr	87	76.71313	555	100	54	120	60	3.5	1.85
Ha	150	80.23899	840	90	49.5	360	80	5	70
Cr	125	96.67344	860	60	70	290	150	6	2.97
Ml	90	99.45852	864	98	57	195	60	10	30
Pe	100	101.4988	867	60	60	265	90	6	8.12
Pa	120	146.1577	900	95	40.5	210	100	5	11.14