

# **Phenology of indigenous and alien vascular flowering plants on sub-Antarctic Marion Island**

by

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## DECLARATION

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Species' seasonal behaviour is of paramount importance in understanding community functioning and dynamics. Recently, plant phenology has further gained significance as a reliable indicator of climate change impacts. Despite the importance of understanding plant dynamics, there are relatively few plant phenological records for the sub-Antarctic region, and where records exist they are often not extensive. Sub-Antarctic Marion Island, typical of Southern Ocean Islands, offers a useful setting for addressing these knowledge gaps. This study documented the vegetative and reproductive phenologies (or aggregate phenological patterns) of twelve indigenous and three alien vascular plant species on the island. The phenological differences among the species and distinct seasonal groupings (e.g. early, intermediate and late species) were examined. I also investigated the phenological differences among the indigenous and alien plant species. Furthermore, the onset of selected reproductive phenophases from the current records was compared with historical records for determining the extent of climate change-related alterations in phenology. Phenological data were collected fortnightly on five, 5 m x 5 m permanent plots per species (except for a few species) for a full growing season. Thus the sample size is  $n = 5$  for all plant species except for *Crassula moschata* ( $n = 4$ ), *Juncus effusus* ( $n=4$ ) and *Rumex acetosella* ( $n=1$ ). Sites of the same species were separated by at least 500 m except for the alien plant, *Juncus effusus*, where all four known populations were selected despite two of these populations being  $< 500$  m apart. This study indicated that Marion Island plants grow throughout the year with no major peaks except in *Azorella selago* and *Acaena magellanica* which showed winter dormancy. However, reproduction in most plant species predominately occurred in spring and summer months. *Pringlea antiscorbutica* and *Poa cookii* were the first two species to set flower buds in September while most species dispersed their seeds in summer except for *Agrostis magellanica* and *Crassula moschata* which dispersed in early autumn. Distinct from most temperate systems, the reproductive seasonality displayed by Marion Island plant species is explained more by daylength than by temperature, perhaps due to the region's typical thermal aseasonality. Interestingly, many co-occurring species and/or clades across the Falkland, Kerguelen, Macquarie and South Georgia Islands also showed similar flowering onset date to the Marion Island plants, further confirming their daylength sensitivity. However, other external factors seem to come into play at later events of reproduction. Consequently, fruit maturation time of similar species across the sub-Antarctic islands varied substantially despite the plants having flowered in the same month. Although plant species showed similar reproductive seasonality, there were significant differences among species

phenologies i.e. phenophase timing, duration and peak occurrence dates. However, using 95% confidence intervals of Generalized Linear Models weighted means, and/or one-way ANOVA (Tukey *post hoc* test), three homogenous sets of species (early, late, or intermediate onsets) were identified based on flower bud, flowering and seed dispersal phenophase onset dates. The homogenous species groupings observed for flower buds also remained unchanged during flowering onset except for *Cotula plumosa* and *Callitriche antarctica* which switched groups. As for the seed dispersal timing, the pattern was not consistent with that of the flower bud and flowering onset homogenous groupings, except for *Acaena magellanica* and *Agrostis magellanica* which remained in the early and late groups, respectively. Conversely, in the case of the timing of other phenophases (pollen release, fruit set and fruit ripening), entire phenophase durations, and peak occurrence dates, species overlapped greatly, resulting in an unbroken progression or continuum of phenology among species. Similarly, the three alien plant species investigated here (*Cerastium fontanum*, *Juncus effusus* and *Rumex acetosella*) showed no consistent phenological differences from the rest of the species. However, a widespread alien plant species on Marion Island, *C. fontanum*, reproduced for most of the year, although its reproduction peak was in summer months as was the case for the rest of the species. This study also indicated that indigenous plant species have altered their reproductive phenologies since 1965. Although the response was species-specific, the majority of plant species significantly delayed the onset of reproductive activities in 2007 by comparison with 1965. However, it is not clear if the observed species response was caused by the now drier and warmer Marion Island climate or by discrepancies in reporting in the earlier studies and/or sampling differences between the recent and historical records. Therefore, these results should be taken with caution. In conclusion, this research provided a detailed phenological dynamics record for vascular plant species on the island. Over time these records may be used as a basis for monitoring and modelling the impact of climate on plant phenology on the island.

Spesies se seisoenale gedrag is van die allergrootste belang in die begrip van gemeenskapsfunksionering en dinamika. Meer onlangs het plant fenologie verdere betekenis verwerf as 'n betroubare indikator vir die impakte van klimaatsverandering. Ondanks die belangrikheid om plant dinamika te verstaan, is daar relatief min plant fenologiese rekords vir die sub-Antarktiese streek en waar rekords wel bestaan is dit dikwels nie omvangryk nie. Sub-Antarktiese Marion Eiland, tipies van Suidelike Oseaan Eilande, bied 'n nuttige ligging om hierdie kennis gapings aan te spreek. Hierdie studie het die vegetatiewe en voorplantingsfenologieë (of gesamentlike fenologiese patrone) van elf inheemse en drie uitheemse vaatplant spesies op die eiland gedokumenteer. Die fenologiese verskille tussen die spesies en duidelike seisoenale groeperings (bv. vroeë, intermediêre en laat spesies) is ondersoek. Ek het ook die betekenisvolle fenologiese verskille tussen die inheemse en uitheemse plantspesies ondersoek. Voorts, die aanvang van gekose voortplanting feno-fases van huidige rekords is vergelyk met historiese rekords om die mate van klimaatsverandering verbandhoudende veranderinge in die fenologie te bepaal. Fenologiese data is twee weekliks ingesamel op vyf, 5 m x 5 m permanente plote per spesie (behalwe vir 'n paar spesies) vir 'n volle groei seisoen. Dus, die insamelings grootte is  $n = 5$  vir al die plantspesies behalwe vir *C. moschata* ( $n = 4$ ), *Juncus effusus* ( $n=4$ ) en *Rumex acetosella* ( $n=1$ ). Persele vir dieselfde spesies is geskei deur ten minste 500 m, behalwe vir die uitheemse plant, *Juncus effusus*, waar al vier populasies wat bekend is gekies is, ten spyte daarvan dat twee van hierdie populasies < 500 m uitmekaar is. Hierdie studie het aangedui dat Marion Eiland plante regdeur die jaar groei, met geen belangrike spitstye nie, behalwe in *Azorella selago* en *Acaena magellanica* wat 'n winter rusperiode wys. Hoe ookal, voortplanting in meeste van die plantspesies het hoofsaaklik voorgekom tussen die lente en somermaande. *Pringlea antiscorbutica* en *Poa cookii* was die eerste twee spesies om blomknoppe uit te stoot in September, terwyl die meeste spesies hulle sade versprei het gedurende die somer, behalwe vir *Agrostis magellanica* en *Crassula moschata* wat versprei het in vroeg herfs. Duidelik van meeste gematigde sisteme, word die voortplanting seisoenaliteit, getoon deur die Marion Eiland plantspesies, verduidelik meer deur dag-lengte as deur temperatuur, moontlik weens die streek se tipiese termiese a-seisoenaliteit. Interessant, baie spesies en/of afstameling-groeperings wat saam aangtrek word dwarsoor die Falkland, Kerguelen, Macquarie en Suid Georgia Eilande wys ook soortgelyke bloei aanvangsdatums as die Marion Eiland plante, nog meer bevestigend van hulle dag-lengte sensitieweiteit. Hoe ookal, ander eksterne faktore blyk betrokke te raak by latere gebeure van

voortplanting. Gevolglik het vrug rypwordingstyd van dieselfde spesies oor die sub-Antarktik noemenswaardig verskil, ten spyte daarvan dat die plante in dieselfde maand geblom het. Alhoewel plantspesies dieselfde voortplanting seisoenaliteit gewys het, was daar 'n noemenswaardige verskil tussen spesie fenologieë, m. a. w. feno-fase tydsberekening, tydsduur en spits voorkomsdatums. Hoe ookal, deur gebruik te maak van 95% betroubaarheid intervalle van Algemene Lineêre Modelle gewigte gemiddelde en/of een rigting ANOVA (Turkey post hoc toets), is drie homogene stelle van spesies (vroeë, laat en intermediêre aanvang) geïdentifiseer gebaseer op blomknop, bloei en saad verspreiding feno-fase aanvangsdatums. Die homogene spesie groeperings waargeneem op blomknoppe het ook onveranderd gebly gedurende bloei aanvang behalwe vir *Cotula plumosa* en *Crassula antarctica* wat groepe geruil het. Vir die saadverspreiding tydsberekening was die patroon nie konstant met die van die blomknop en bloei aanvang homogene groepe nie, behalwe vir *Acaena magellanica* en *Agrostis magellanica* wat in die vroeë en laat groepe respektiewelik gebly het. Omgekeerd, in die geval van tydsberekening van ander feno-fases (stuifmeel vrysetelling, vrugwerp, vrugrypwording), volledige feno-fase tydsduur en spits voorkomsdatums het spesies grootliks oorvleuel, wat 'n ongebroke vordering of deurlopendheid van fenologie tussen die spesies tot gevolg het. Ooreenkomstig het die drie uitheemse spesies wat hier ondersoek is (*Cerastium fontanum*, *Juncus effusus* en *Rumex acetosella*) geen bestendige fenologiese verskille van die res van die spesies gewys nie. Hoe ookal, 'n wydverspreide uitheemse spesie op Marion Eiland, *Cerastium fontanum*, het deur die meeste van die jaar voortgeplant, hoewel met 'n voorplanting spits in die somer maande soos die res van die spesies. Hierdie studie dui ook aan dat inheemse plantspesies hulle voortplanting fenologieë verander het sedert 1965. Alhoewel die reaksie spesie-spesifiek was, het die meerderheid van die plantspesies hulle voortplanting aanvang aansienlik vertraag gedurende 2007 in vergelyking met 1965. Hoe ookal, dis nie duidelik of die waargeneemde spesie reaksie was as gevolg van die nou droër en warmer Marion Eiland klimaat of deur teenstrydighede in verslagewing gedurende die vroeë studies en/of insameling verskille tussen die onlangse en historiese rekords. Daarom moet hierdie resultate met versigtigheid hanteer word. In samevatting, hierdie navorsing voorsien 'n gedetailleerde fenologiese dinamieka rekord vir vaatplantspesies op die eiland. Oor tyd kan hierdie rekords gebruik word as basis vir monitering en modellering van die impak van klimaat.

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Phenology refers to the study of the timing of an organism's life-history events in relation to both biotic and abiotic factors (Kushwaha & Singh, 2008). Typical examples of plant phenology include the timing and duration of leaf emergence, flowering, fruiting and dispersal. Amongst other abiotic factors, the most important factors regulating the timing of these phenophases are temperature (IPCC, 2001; Ahas & Aasa, 2006; Khanduri *et al.*, 2008), photoperiod (van Dijk & Hautekeete, 2007) and precipitation (Jentsch *et al.*, 2009). Nevertheless, no abiotic factor triggers plant phenology individually - factors work synergistically or at least overlap (Rathcke & Lacey, 1985; Berg *et al.*, 2008). For example, in high latitude communities such as Alpine and Arctic habitats, temperature together with photoperiod and rainfall regulate the melting of the snow, which in turn determine the start of the plant growing season (Molau, 2005; Berg *et al.*, 2008). However, the extent to which species require these environmental cues is also species, phenophase and geographic location-specific (Spano *et al.*, 1999; Menzel, 2002; Putterill *et al.*, 2004; Molau *et al.*, 2005).

### **Climate and Phenology**

Climate governs the distribution and seasonal behaviour of species. By facilitating the role that other cues play, temperature is regarded as a major cue for plant phenology particularly in temperate systems (Rathcke & Lacey, 1985; Fitter *et al.*, 1995; Hao *et al.*, 2006; Tooke & Battey, 2010). For instance, some plants in temperate regions first require exposure to chilling temperatures before initiating their growing season. This vernalisation process is of fundamental importance in facilitating chemical reactions for vegetative and reproductive development (Chuine & Beaubien, 2001; Putterill *et al.*, 2004; Hänninen *et al.*, 2007). On the other hand, there are some plant species whose phenology is more responsive to photoperiod than to temperature (Lin, 2000; Putterill *et al.*, 2004; van Dijk & Hautekeete, 2007). It has been shown experimentally that these species need at least one day of optimum photoperiod for growth or developmental activities to be stimulated (Corbesier *et al.*, 1996; Purohit & Ranjan, 2002). Precipitation is also one of the cues that regulate plant phenology. However, it is more influential in water limited systems (Weltzin *et al.*, 2003; Okullo *et al.*, 2004; Dreyer *et al.*, 2006) than in temperate systems because water is not typically limiting in the latter (Peñuelas *et al.*, 2004).

## Climate Change and Phenology

Global mean air temperature and the frequency of drought and floods have increased since 1970's, with many areas becoming either warmer and wetter or warmer and drier (IPCC, 2007). Warmer and wetter/drier climates often create conditions that species are not well adapted to (Hulme & Viner, 1998; Cayan *et al.*, 2008a, b). As an adaptive response species may shift their ranges poleward and/or change their seasonal behaviour to track their suitable climate envelopes, failure of which will render them extinct. However, the response varies amongst species and even between individuals sharing the same habitat (Corlet & Lafrankie, 1998; Fitter & Fitter, 2002; Rosenzweig *et al.*, 2008). For example, warmer springs are causing spring events of many temperate plants to occur earlier i.e. leaf-bud burst or blooming date (Myeni *et al.*, 1997; Bertin, 2008; Hülber *et al.*, 2010). At the same time events in other plant species are occurring later than was typical of their species while others have retained their phenology (Fitter & Fitter, 2002; Parmesan & Yohe, 2003). Generally, trends are showing that warmer temperatures are responsible for earlier phenology in temperate systems. However, the synergistic impact of extreme precipitation events and warming might complicate this trend (Jenstch *et al.*, 2009). The only plant species that are expected to retain their phenology despite massive changes in temperature and precipitation are those largely responsive to photoperiod because photoperiod hasn't changed over time (Thuiller, 2007; Rosenzweig *et al.*, 2008). If a shift in one or more events of species life-history is not complimented by a shift in phenology of interacting species this may be disastrous to species survival (Memmot *et al.*, 2007; van Asch & Visser, 2007). For example, asynchrony between a plant and pollinator might have major repercussions for the reproduction success of the plant and survival of the pollinator (Harrington *et al.*, 1999; Visser & Holleman, 2001; van Asch & Visser, 2007).

Regrettably, most of the published evidence about climate change-necessitated phenological shifts originates from the Northern Hemisphere owing to lack of long-term data to use as a basis for such investigations in Southern Hemisphere (Wolfe *et al.*, 2005; Thuiller, 2007; Rosenzweig *et al.*, 2008). Results obtained from the Northern Hemisphere alone may not necessarily represent a global biotic response (Root *et al.*, 2003; IPCC, 2007; Thuiller, 2007). However, poor documentation in the Southern Hemisphere should not be confused with lack of species response (see Heumann *et al.*, 2007; Jarrad *et al.*, 2008; Petrie & Sadras, 2008; Rosenzweig *et al.*, 2008; Gallagher *et al.*, 2009). Yet it should be noted that insufficient evidence exists for the region to identify general phenological trends, which provides a strong argument for the establishment of a phenological network or at least greater emphasis on such work in the Southern Hemisphere (Kushwaha & Singh,

2008; Rosenzweig *et al.*, 2008). Amongst other areas in the Southern Hemisphere, the high latitude regions including their ocean islands also are characterized by a relative paucity of phenological records (Rosenzweig *et al.*, 2008).

### **Phenological Observations in the sub-Antarctic Region**

Sub-Antarctic islands represent the only terrestrial landmasses in a vast Southern Ocean (de Villiers *et al.*, 2006). Because of similar climate and historical settings, most islands in the sub-Antarctic region share many taxa (Chown *et al.*, 1998; Frenot *et al.*, 2001, 2005). Isolated as these islands might be from the other terrestrial systems they provide a good opportunity for answering various research questions (Bergstrom & Chown, 1999). Due to their conservation value sub-Antarctic islands have been declared protected areas by their respective claimant nations (de Villiers *et al.*, 2006). Although there are no long-term plant phenological data sets on sub-Antarctic region, some phenological observations have been undertaken to simply understand the climate-species relationship or species reproductive biology. Specifically, these records exist for South Georgia (Tallowin, 1971; Walton, 1975, 1977, 1982), Kerguelen (Werth, 1911; Dorne, 1977; Frenot & Gloaguen, 1994; Aubert *et al.*, 1999), Macquarie (Taylor, 1955; Bergstrom *et al.*, 1997), Prince Edward (Huntley, 1970) and Falkland Islands (Moore, 1968; Broughton & McAdam, 2005) vascular plant species. However, for most of these islands the studies have not been extensive and have either focused on few components of species life-history or studied only a limited range of species. For example, only the timing of selected reproductive events (mostly flowering) has been investigated ignoring phenophase interdependence.

Over the last five decades, there has been a substantial change in sub-Antarctic climate (Bergstrom & Chown, 1999). These changes have been accompanied by considerable changes in some aspects of plant biology (e.g. le Roux & McGeoch, 2008a). However, these changes have not been investigated from the perspective of phenology despite the fact that it is highly responsive to slight changes in climate (Wolfe *et al.*, 2005; Rosenzweig *et al.*, 2008). In areas like the sub-Antarctic where long term data doesn't exist, using any phenological information available to monitor environmental change might provide an idea about the direction of any phenological shift.

### **Marion Island**

The first detailed vegetation survey on Marion Island was conducted by Huntley in 1965. He investigated the ecology, distribution, phenology and community structure of vascular plants

(Huntley, 1971). Similar to other islands, this survey paved a way for a number of plant studies (e.g. Gremmen, 1975; Gremmen *et al.*, 1998; Gremmen & Smith, 1999; Smith *et al.*, 2001; le Roux & McGeoch, 2008a) but this never extended to comprehensive and systematic plant phenology. Furthermore, Huntley's phenological records remain the first and only plant phenology on the island, forming a potential basis for investigating phenological changes. Studying plant phenology on sub-Antarctic Marion Island will provide much-needed data for this region, to understand climate change effects (see also Bergstrom & Chown, 1999; Smith, 2002), and for the Southern Hemisphere more generally.

Therefore the current research has two major aims:

- To document the aggregate phenologies of 15 vascular plants on Marion Island
- Examining changes in plant phenology over the past 42 years since Huntley's original study

In addressing these aims the following major questions will be addressed:

### **1) Different plant species have different phenology**

Due to idiosyncratic responses of species to the same environmental cue there may be no overall trend or seasonality in Marion Island plant phenology. Fifteen plant species were studied and therefore it can be expected that not all these species will have identical phenologies (Castro-Díez *et al.*, 2003; Bolmgren & Cowan, 2008). Furthermore, by observing phenological shifts over 42 years, different species may have differential responses to the changing climate (Fitter & Fitter, 2002; Parmesan & Yohe, 2003).

### **2) Alien and indigenous plants display different phenology**

Other studies have shown that alien plants flower earlier or later than indigenous plants depending on climatic condition in their new range (Daehler, 2003; Godoy *et al.*, 2009). Irrespective of earlier or later flowering, faster growth rates that individual alien plants possess allow them to complete their life-cycle earlier than natives to reduce competition (see Daehler, 2003; Sargent & Ackerly, 2008). The null hypothesis examined here is that invasive plants flower simultaneously with natives (see Godoy *et al.*, 2009).

### 3) **Temperature is the overriding factor that influences plant phenology**

As a major driver of phenology, temperature, which has increased on Marion Island over the past half century (le Roux, 2008), could be expected to have resulted in an advancement in plant phenology over this time (Hughes, 2000; Hovenden *et al.*, 2008). Alternatively, other factors such as changes in annual precipitation and relative aseasonality of Marion Island's climate (le Roux, 2008) might also drive phenology (Piao *et al.*, 2006) and therefore influence phenology and the direction of any phenological shift over the last 42 years.

#### **Importance of Phenology**

Traditionally, phenology has been primarily used to understand species' reproductive biology, climate-species relationships and species interactions in a given community (Dech & Nosko, 2004; Gremmen, 2004; Godoy *et al.*, 2009). This information is of fundamental importance in determining the current and potential species ranges in natural habitats and in invaded ranges (Chuine & Beaubien, 2001; Dech & Nosko, 2004; Morin *et al.*, 2007). Recently, the opportunistic existence of long-term phenological records and changes in global climate has further sparked and broadened the scope of phenology to monitoring environmental change impacts on biota (Parmesan & Yohe, 2003; van Vliet *et al.*, 2003; Rosenzweig *et al.*, 2008). Knowing the way in which climate change is currently affecting ecosystem dynamics and functioning will assist with modelling or predicting the extent to which biota might be affected in the future (Chuine & Beaubien, 2001; van Vliet *et al.*, 2003; Morin *et al.*, 2007). Due to the sensitivity of phenophases to slight changes in climate, identifying patterns of variation in plant phenology has become an important task in climate change research (van Vliet *et al.*, 2003; Bowers, 2005).

#### **STUDY AREA**

Marion Island (46°54' S, 37°45' E) is located in the Southern Indian Ocean, north of the Antarctic Polar Frontal Zone (Sumner *et al.*, 2004). Jointly with other islands that surround the Antarctica continent, Marion Island forms a sub-Antarctic biogeographic region. Marion Island is isolated from other landmasses and lies 2300 km south-east of Cape Town (Lutjeharms & Ansorge, 2008). The French Crozet Island Group, Île aux Cochons a fellow member of sub-Antarctic biogeographical region lies only 950 km away to the east (Chown & Froneman, 2008). Marion Island and Prince Edward Island form the Prince Edward Islands Group and are only separated by 19 km, with Marion Island, the larger of the two, covering an area of approximately 290 km<sup>2</sup> (Chown &

Froneman, 2008). This island is a volcanic landmass formed roughly 500 000 years ago (McDougall *et al.*, 2001).

Like many oceanic islands, Marion Island experiences a hyper-oceanic climate. Strong winds, low temperatures, high precipitation and humidity define the aseasonal climate of most sub-Antarctic islands including that of Marion Island (Bergstrom & Chown, 1999; le Roux, 2008; le Roux & McGeoch, 2008b). There is a little variation in the diurnal temperatures of both winter and summer months on Marion Island (Smith & Steenkamp, 1990; le Roux, 2008). Most of the precipitation comes in the form of rainfall, with snow, hail and mist providing a small proportion of total moisture available to organisms. Annual rainfall of about 2000 mm is evenly distributed throughout the year (le Roux, 2008). Wind blows from different directions but the most common and strongest are the north-westerlies, with gale force winds of  $> 15 \text{ m sec}^{-1}$  occurring for more than a quarter of a year (Schulze, 1971; Rouault *et al.*, 2005).

Marion Island's climate has undergone dramatic change, becoming warmer and drier now than it was couple of decades ago. The mean annual air temperature has increased by  $1^{\circ}\text{C}$  between the 1950s and 1990s to  $6.4^{\circ}\text{C}$  from  $5.4^{\circ}\text{C}$  (le Roux & McGeoch, 2008b). Nevertheless, the warmest years ever recorded were between 1996 and 1999 (Smith, 2002). This increase in temperature was also accompanied by a decline in annual precipitation from an average of 3000 mm in 1960's to 1 975 mm in 1990's (Bergstrom & Chown, 1999; le Roux & McGeoch, 2008b). At the same time changes in precipitation patterns and frequencies were recorded. Sunshine hours have increased on average by 3.3 hours a year (Smith, 2002). Warmer temperatures in conjunction with longer sunshine hours and drastic changes in precipitation patterns and amount, may have led to the disappearance of the permanent snowline at an altitude of 600 m a.s.l where it occurred in the 1960's (Sumner *et al.*, 2004). Currently the permanent snowline occurs at an altitude of  $> 1000 \text{ m a.s.l.}$ , 400 m higher than in 1960's (Sumner *et al.*, 2004).

Marion Island is home to 23 indigenous and 12 introduced vascular plant species, 90 mosses and 44 liverworts (Gremmen & Smith, 2008). Some of these species are endemic to the sub-Antarctic region. The combination of vascular plants and bryophytes co-exist in a variety of vegetation communities depending on soil nutrients, soil type, moisture content, salinity and wind exposure. These are Mire Complex, Slope Complex, Fellfield Complex, Polar Desert, Coastal Salt-spray Complex and Biotic Complex (Gremmen & Smith, 2008). Nutrients available to the plants come

mostly from marine seals and birds that seasonally breed and moult on the island (Gremmen & Smith, 2008).

## **STUDY SPECIES**

A total of 15 vascular plant species have been selected for this study. The majority of these species are indigenous and only three are alien species on the island. The following species were selected and chosen for the phenological studies:

### ***Acaena magellanica* Lam. Vahl. (Rosaceae)**

*Acaena magellanica* is a perennial, herbaceous plant indigenous to sub-Antarctic islands, occurring mostly on wind-protected slope habitats (Walton, 1982). However, this woody dwarf shrub can tolerate a range of habitat conditions (Walton, 1976). On Marion Island it reaches optimum growth on Drainage Line communities where it forms dense stands (Gremmen *et al.*, 1998). As a creeper, stems harbouring large green leaves with a touch of purple colour can grow up to 40 cm in length. Inflorescence stalks can reach a height of 21 cm. This species bears inflorescences that are self-compatible (Walton, 1982). It takes approximately two months for inflorescences at anthesis to develop into matured fruits with spikes suited to animal-facilitated dispersal (Walton, 1982; Hennion & Walton, 1997). However, this species can also spread vegetatively.

### ***Agrostis magellanica* Lam. (Poaceae)**

This is a low-altitude perennial grass indigenous to many sub-Antarctic Islands amongst others; Prince Edward, Macquarie, Falkland, Campbell and Kerguelen Islands. On Marion Island *Ag. magellanica* is dominant on wet and dry mires and may also grow epiphytically on *Azorella selago* cushions (Gremmen & Smith, 2008). Together with *Blechnum penna-marina*, *Poa cookii* and *Azorella selago*; *Ag. magellanica* forms a canopy crop on Marion Island (Smith, 1976). This tuft-forming grass has leaves that are folded and rolled inwards. The size of these leaves varies greatly ranging from 5-45 cm. Green- and purple-coloured inflorescences during spring could be seen from a distance and in other cases are overgrown by leaves.

### ***Azorella selago* Hook. f. (Apiaceae)**

*Azorella selago* is a long-lived and slow-growing cushion plant, indigenous to most sub-Antarctic islands. On most of these islands *A. selago* is a keystone species (Hugo *et al.*, 2004; le Roux & McGeoch, 2004). This cushion plant is also a pioneer species during vegetation succession on



Marion Island (Yeloff *et al.*, 2007; Gremmen & Smith, 2008). *Azorella selago* is ubiquitous on Marion Island and is the only vascular plant species that can grow and reproduce up to 840 m a.s.l., this is far beyond the altitudinal limit of other vascular plants (Huntley, 1970; le Roux & McGeoch, 2008a). However, it dominates the Fellfield vegetation communities. During spring this plant bears greenish-yellow flowers. Changes in precipitation pattern may lead to major changes in life-cycle history of this cushion plant (Frenot *et al.*, 1997; le Roux *et al.*, 2005) which in turn might affect other species that depend on it for resources and shelter.

***Blechnum penna-marina* Poir. Kuhn (Blechnaceae)**

*Blechnum penna-marina* is an indigenous fern on Marion Island (Smith, 1976). Like many ferns, *B. penna-marina* prefers habitats that are well protected from the wind and often forms a dense spongy carpet in this habitat. Graminoids, *A. selago* and *Ac. magellanica* may form part of the Slope Complex vegetation community that *B. penna-marina* dominates (Gremmen & Smith, 2008). Mature fronds are sensitive to frost and very low temperatures may also lead to their death. Fertile fronds which do not last beyond autumn season are more prone to frost than vegetative ones (Bannister, 1984).

***Callitriche antarctica* Engelm. ex Hegelm. (Callitrichaceae)**

*Callitriche antarctica* is an annual to perennial indigenous plant on some sub-Antarctic islands including Marion Island. As a nitrophile, *C. antarctica* is predominately found on biotically nitrogen-enriched coastal mud habitats and sometimes forms hanging carpets on seal wallows (Whinam, 1989; Vidal *et al.*, 2003). The distribution of this species is restricted to coastal areas up to 50 m inland on the eastern side of Marion Island but on the northern and southern side extend up to 300 m towards the interior (Gremmen & Smith, 2008). Opposite leaves of this creeper are fleshy and fragile with margins that are well rounded. *Callitriche antarctica* is characterised by both vegetative and sexual mode of reproduction. Sexually, flowers can either be solitary, axillary or diecious. These flowers exhibit a geitonamous pollination system where self-fertilisation occurs through anemophily (Philbrick & Anderson, 1992; Philbrick & Les, 2000; Ackerman, 2000) or hypohydrophily (Philbrick, 1993) depending on the habitat. After pollination, it sets hard-rounded green fruits of about 1-1.5 mm in length and breadth.

***Cerastium fontanum* L. (Caryophyllaceae)**

*Cerastium fontanum* is a European perennial weed common and widespread on sub-Antarctic islands (Walton, 1975). On Marion Island, *C. fontanum* has spread away from its point of introduction to distant disturbed and non-disturbed habitats, and on most of the sub-Antarctic islands where it occurs has become naturalised and widespread (Walton, 1975; Gremmen & Smith, 1999; Gremmen, 2004). This plant harbours plenty of solitary flowers resulting in many egg-shaped seeds from individual capsule (Walton, 1975; Bergstrom & Smith, 1990; Gremmen, 2004). Like many invaders, the success of this species on the sub-Antarctic region might be attributed to its versatile reproduction biology.

***Cotula plumosa* Hook. f. (Asteraceae)**

This is a mat-forming, halophilous plant species indigenous on most sub-Antarctic islands (Turner *et al.*, 2006). On Marion Island, *Cotula plumosa* grows in both Biotic Complex and Coastal Salt-spray habitats. However, the rosette size differs based on salt-spray exposure and biotic soil nutrients. For instance, where there is frequent inundation by ocean waves rosettes are normally short and compact but where the soil is biotically enriched with nitrogen, rosettes are large and fragile (Turner *et al.*, 2006; Gremmen & Smith, 2008). This species produces many seeds which are dispersed by wind and animals (Turner *et al.*, 2006) but it also has the ability and means to reproduce from stolons.

***Crassula moschata* Forst. f. (Crassulaceae)**

*Crassula moschata* is also a halophilous plant species which is tolerant to frequent salt deposition (Huntley, 1971). In many cases, *C. moschata* co-occurs with *C. plumosa* on Coastal Salt-spray vegetation communities, more especially at rocky coastal sites. The structure and functioning of this species is to a larger extent controlled by a combination of marine and terrestrial abiotic activities (Huntley, 1971).

***Juncus effusus* L. (Juncaceae)**

*Juncus effusus* is a dense, tuft-forming rush of about 1.5 m in height. The plant is indigenous in the Northern Hemisphere mostly on edges of nutrients-rich wetlands or marshes (Wetzel & Howe, 1999; Smolders *et al.*, 2008). Its exact year of introduction is not known for Marion Island. Currently, this species has four populations on Marion Island: one at Trypot beach, two at Ship's Cove and one along the banks of van den Boogaard river, roughly close to the meteorological

station. These populations have not shown any signs of expansion or colonising other areas since they were first recorded by Huntley in 1965. This may be due to the fact that this plant doesn't produce viable seeds (Gremmen, 2004); however in its native range the plant can form uniform stands through rhizomes (Wetzel & Howe, 1999).

***Montia fontana* L. (Portulacaceae)**

*Montia fontana* is a fast growing, mat-forming annual to perennial herb with very short growing season (Walton, 1982; Bergstrom *et al.*, 1997). This indigenous species is common on coastal areas which are biotically influenced and may co-exist with *C. antarctica*, *P. annua* and *P. cookii* (Gremmen & Smith, 2008). Greenish-white solitary flowers of 2-3 mm in diameter develop between a leaf and apical part of single stem. Depending on habitat conditions this homogamous species may self-pollinate and/or display self-compatibility fertilization (Walton, 1982). When seeds are ready for dispersal, capsule dehisces explosively to expose or drop three dark brown to black seeds.

***Poa cookii* Hook. f. (Poaceae)**

This indigenous grass species is common on habitats that are biotically influenced by seal and seabird activities (Vidal *et al.*, 2003; Gremmen & Smith, 2008). Quite often it forms dense and large tussocks in this habitat. However, in habitats with a lower incidence of biotic activities it hardly reaches optimum growth (Huntley, 1971; Vidal *et al.*, 2003). The most distinguishing characteristic of species belonging to a *Poa* is their folded, flat and large green leaves surrounding the culm throughout the year. Light-green florets are unevenly distributed on 5-25 cm cylindrical panicle i.e. they are more clustered on the apical part of inflorescence than at the bottom. Spikelets on both ends of the inflorescence produce both male and female flowers but anthers at the apical part are larger.

***Pringlea antiscorbutica* R. Br. (Brassicaceae)**

Also known as Kerguelen cabbage, *P. antiscorbutica* is a long-lived perennial plant endemic to sub-Antarctic islands (Hennion & Walton, 1997; Chapuis *et al.*, 2000). The ability of this species to withstand various harsh climatic conditions enables it to survive and reproduce on variety of vegetation communities from very low to high altitude (Hennion & Walton, 1997; Hennion & Bouchereau, 1998). From a seedling this plant needs at least three years to start flowering and when it does, may self-pollinate to set many viable seeds that may be dispersed to remote locations by

various agents including water (Hennion & Walton, 1997; Chapuis *et al.*, 2000; Schermann-Legionnet *et al.*, 2007).

***Ranunculus biternatus* Sm. (Ranunculaceae)**

*Ranunculus biternatus* is a perennial, herbaceous plant indigenous to Southern Indian Ocean Islands, mostly on low-altitude waterlogged habitats. This species produces solitary flowers with yellow petals which are able to self-fertilize (Hennion & Walton, 1997). However, it has the ability and means of growing vegetatively through stolons.

***Rumex acetosella* L. (Polygonaceae)**

*Rumex acetosella* is a perennial plant exotic to sub-Antarctic islands such as Marion, Crozet, South Georgia, Kerguelen, Auckland and Campbell Islands (Walton, 1975). On Marion Island it grows in biotically influenced low-altitude habitats, close to the coastline. This species has remained restricted to its points of introduction close to meteorological station and at Goney Plain, despite its long residence time (Gremmen & Smith, 1999; Gremmen, 2004). The morphology, colour and size of leaves and flowers of this weedy perennial plant are greatly influenced by climatic condition of the area of occurrence (Harris, 1970). In most habitats this plant appears reddish with fine soft greyish hairs on stems and leaves. When conditions are favourable it produces abundant and dense stands of reddish, maroon or yellowish dioecious flowers with high chances of setting seeds (Walton, 1975; Gremmen & Smith, 1999). Currently, vegetative growth and spread appear to be sustaining the *R. acetosella* populations on Marion Island (Gremmen, 2004).

***Uncinia compacta* R. Br. (Cyperaceae)**

*Uncinia compacta* is a moisture and temperature sensitive sedge which is under threat from mice which feed on its matured seeds immediately when they ripe on Marion Island (Chown & Smith, 1993). The sedge is well distributed on dry mires on Marion Island. This species reproduce seeds with hooks which enable them to stick with ease on animals and be dispersed to distant locations (Hennion & Walton, 1997).

*Poa annua* was not studied because large stands were not found in the study area. Habitats previously dominated by *P. annua* now seem to be composed of *Agrostis stolonifera*.

## **THESIS OUTLINE**

Four chapters constitute this thesis. The first chapter is the general introduction to plant phenology globally and in the sub-Antarctic region. Chapter two focuses on the individual species phenology. Here, the growth and reproductive phenophase timing, duration and peak occurrence dates are provided. In addition, the reproductive phenophase timing, duration and peak occurrence dates are compared between species to determine significant differences. The third chapter examines the impact of climate change on the timing of selected reproductive events by comparing Huntley's (1970) 1965/66 records and the current records. Only indigenous species whose historical phenological record exists on the island are used for the comparison. The fourth and final chapter of this research thesis summarises the findings and provides indications of future research requirements.

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**INTRODUCTION**

Phenology refers to the study of timing of an organism's life-history and behaviour in relation to biotic and abiotic factors. In flowering plants, typical examples include the study of timing of leaf emergence, flower set, full-bloom, fruit set and the seed dispersal phenophases. These phenophases occur in sequential order and their respective occurrence is dependent on the timing of the preceding events (Donohue, 2002; Sola & Ehrlén, 2007). For example, flowering activity is partly or wholly linked to vegetative phenology such that plants which initiate their growth early in the season also commence flower development earlier (Cleland *et al.*, 2006). Therefore, measures of phenology should consider both the growth and reproduction phenophases, thereby acknowledging their interdependence. An aggregate/detailed phenological study may also provide an indication of how a species utilizes and allocates variable resources towards its vegetative growth and flower development (Castro-Díez *et al.*, 2003; Golluscio *et al.*, 2005; Iversen *et al.*, 2009). Irrespective of specific plant species life-history strategies (rapid or slow), the timing of events is an important component of any species survival and distribution (Rathcke & Lacey, 1985; Chiuine & Beaubien, 2001; Morin *et al.*, 2007). For example, for species to reproduce successfully in a given area the timing of growth and reproductive events has to coincide with optimum resource (abiotic or biotic) availability (Rathcke & Lacey, 1985). A mismatch, particularly in the timing of bloom, may have negative consequences for not only the species' survival, but perhaps also for the existence of other interacting species (Waser, 1979; Visser & Holleman, 2001). In consequence, phenology forms a significant tool in understanding community functioning.

Important as phenology is, few phenological records exist for the temperate Southern Hemisphere and particularly for the sub-Antarctic region (e.g. see data listing in Rosenzweig *et al.*, 2008). Their absence is especially concerning given the fact that climate change may differentially affect Southern and Northern Hemisphere systems (Bergstrom & Chown, 1999; Chown *et al.*, 2004; le Roux & McGeoch, 2008a). The relatively small number of phenological investigations conducted in the sub-Antarctic have either focused on a limited set of events or on few species, that are perhaps not always fully representative of the island vegetation community (see Werth, 1911; Tallwin, 1971; Walton, 1977b, 1982; Dorne, 1977; Frenot & Gloaguen, 1994). For example, on South Georgia, Walton (1982) observed the reproductive phenology of alien and indigenous species with

much emphasis on onset dates of flowering, pollen release and fruiting. For Macquarie Island, Bergstrom *et al.* (1997) provided information on reproductive phenology of 10 vascular plant species. On Kerguelen Island only the growth and reproductive phenology of seven plant species has been documented (Dorne, 1977). Similarly, limited information is available on plant phenology on sub-Antarctic Marion Island. Baseline studies highlighting the timing of reproductive events for the indigenous (Huntley, 1970) and some of the alien vascular plant species have been undertaken (see Gremmen & Smith, 1999; Gremmen, 2004). Likewise, investigations of primary productivity have emphasized the prolonged growing season of vascular plants and bryophytes on the island (Smith, 1987, 1988). Despite the somewhat limited nature of these studies, they provide a useful baseline set of expectations for more detailed plant phenological studies on the island. However, to date, no comprehensive plant phenological studies have been undertaken, and thus much information on the timing of events (including the species-climate relationship) and reproductive ecology remains missing, despite the significance of such information for understanding plant community dynamics and its responses to climate change. Indeed, given the pace of climate change in the region (Bergstrom & Chown, 1999; le Roux, 2008), and the significance of phenological change as an indicator of the nature of climate change impacts (Parmesan, 2007; Post *et al.*, 2008; Rosenzweig *et al.*, 2008), the absence of such baseline information is problematic.

To address this situation, the timing, peak dates and duration of aggregate life-history events should be measured over a full growing season (Fenner, 1998). In other words, a comprehensive and systematic vascular plant phenology taking into account vegetative and reproductive events of both alien and indigenous species representative of the community may provide a clearer picture of temporal structure, resource dynamics and seasonality of Marion Island plants, both to improve current understanding and help to understand the likely influence of climate change. Therefore, this study was undertaken to: (i) document the vegetative and reproductive phenologies (or aggregate phenological patterns) of twelve indigenous and three alien vascular plant species on Marion Island; (ii) examine the differences found among the species and whether distinct seasonal groupings (e.g. early and late species) could be identified; and (iii) determine whether significant differences in phenology among the indigenous and alien plant species could be identified. Although comparison with earlier work on the reproductive phenology of a subset of these species (see Huntley, 1970) is possible, this comparison will follow in the next Chapter.

## MATERIALS AND METHODS

### Study Site

The study was conducted on sub-Antarctic Marion Island (46°54'S, 37°45'E), a member of Prince Edward Islands Group. Marion Island, the larger of the two islands, is a young, volcanic island (500 000 years old, McDougall *et al.*, 2001) of about 290 km<sup>2</sup> in size with a maximum altitude of 1230 m above sea-level (Chown & Froneman, 2008). As an oceanic island, Marion Island has a typically hyper-oceanic climate that is thermally stable (le Roux, 2008; le Roux & McGeoch, 2008b). Rainfall constitutes more than 90% of the moisture available to organisms, particularly at low altitudes (le Roux, 2008). At high altitudes, snow is a common occurrence while at low altitude snow falls occasionally during winter months. The climate, geological structure and isolation of this island has resulted in a species-poor system characterised by few vascular plant life-forms, such as herbs, a dwarf shrub, grasses, sedges, rushes, ferns and cushion plants (Gremmen & Smith, 2008). A large proportion of the nutrients available to plants originate from seals and seabirds that seasonally breed on the island, and the other fraction comes from organic matter decomposition (Smith & Froneman, 2008).

### Study Species and Description

This study documented the phenology of three alien and 12 indigenous vascular plant species, namely: Indigenous: *Acaena magellanica*, *Agrostis magellanica*, *Azorella selago*, *Blechnum pennamarina*, *Callitriche antarctica*, *Cotula plumosa*, *Crassula moschata*, *Montia fontana*, *Pringlea antiscorbutica*, *Poa cookii*, *Ranunculus biternatus*, and *Uncinia compacta*; Alien: *Cerastium fontanum*, *Juncus effusus* and *Rumex acetosella*.

#### ***Acaena magellanica* Lam. Vahl. (Rosaceae)**

The high plasticity that this species possesses makes it tolerant to various habitat conditions at altitudes up to 552 m on Marion Island (Huntley, 1970, le Roux & McGeoch, 2008a). The species may survive in either wet, dry or mesic habitats often achieving optimum growth on Drainage Line slopes (Gremmen *et al.*, 1998). Due to the deciduous nature of this shrub, leaves produced in spring senescence at the end of the growing season. February is the month in which the aboveground biomass of live leaves peaks, whereas aboveground necromass increases two months earlier (Smith, 1987). Flower buds set early in the season after a substantial increase in day length (Huntley, 1970),

and the maximum reproductive biomass is reached between December and January (Smith, 1987; 1988).

***Agrostis magellanica* Lam. (Poaceae)**

*Agrostis magellanica* has a widespread distribution on Marion Island occurring from the coast to approximately 743 m a.s.l. (Huntley, 1970; le Roux & McGeoch, 2008a), but prefers low-altitude sites with high moisture, i.e. Mire vegetation communities (Gremmen & Smith, 2008). This grass may also grow epiphytically on *A. selago* cushions. Together with *Acaena magellanica*, *Azorella selago*, *Blechnum penna-marina* and *Poa cookii*, this species dominates the standing crop of vascular plants on Marion Island (Smith, 1976). The flowering phenology of this hygrophilous species commences between November and December, months after the considerable increase in daylength (Huntley, 1970). Leaf senescence follows three months later from March to April where dead leaves detach from culms and are often carried away by strong winds.

***Azorella selago* Hook. f. (Apiaceae)**

Growing as a distinct cushion or continuous mat, *A. selago* is ubiquitous and widespread on Marion Island, occurring from sea-level up to 840 m (Huntley, 1970; le Roux & McGeoch, 2008a; Mortimer *et al.*, 2008). Despite the cushion's omnipresent distribution on Marion Island, *A. selago* dominates the Fellfield vegetation communities. Moreover, the cushion has proved to be an important species on Marion Island by providing habitats for other plant species (Huntley, 1971; Frenot *et al.*, 1998; le Roux *et al.*, 2005) and something of a resource oasis for invertebrates (Barendse & Chown, 2001; Hugo *et al.*, 2004). The plant starts to recover from winter recess by developing leaf buds from July and by early summer the rest of the cushion is covered with matured leaves. This is followed by development of flower buds during mid-September. Leaf discolouring is initiated in March lasting until May when almost the whole cushion appears brown (Smith, 1987). The phenology of this species is more responsive to photoperiod than any other cue, thus setting flowers by mid-September.

***Blechnum penna-marina* Poir. Kuhn (Blechnaceae)**

*Blechnum penna-marina* dominates slope habitats with less incidence of wind or salt-spray (Gremmen & Smith, 2008). These conditions are often met on low elevation (< 300 m a.s.l.) inland slopes giving rise to the Closed Fernbrake vegetation community (Gremmen & Smith, 2008). In other habitats, such as Open Fernbrake, the plants are sparser. Vegetative fronds continuously

emerge from the litter carpet from late September to April. As expected, the earliest fronds are typically the first to die-off in January. Fertile fronds, that are often taller than vegetative fronds, appear by late December. Depending on the habitat, aboveground biomass for both vegetative and reproductive fronds peaks in March, May or June. Moreover, living biomass substantially declines in winter (Smith, 1987). The largest percentage of aboveground standing crop is normally comprised of dead litter.

***Callitriche antarctica* Engelm. ex Hegelm. (Callitrichaceae)**

*Callitriche antarctica* grows as a nitrophile in nutrient-enriched coastal habitats with high moisture levels and often forms hanging carpets (Whinam, 1989; Vidal *et al.*, 2003, le Roux & McGeoch, 2008a). On the eastern side of Marion Island *C. antarctica* pre-dominantly grows from approximately 0 m to 50 m inland (Gremmen & Smith, 2008). However, the species has an altitudinal limit of 535 m island wide (le Roux & McGeoch, 2008a). Flowering activity that occurs seasonally by late September is cued by combined effects of daylength and temperature (Huntley, 1970).

***Cerastium fontanum* L. (Caryophyllaceae)**

*Cerastium fontanum* is an alien, short-lived perennial weed, common and widespread in the sub-Antarctic. The widespread distribution of *C. fontanum* in the region's disturbed and non-disturbed sites is an indication of excellent adaptability (Salisbury, 1961; Walton, 1975; Bergstrom & Smith, 1990; Gremmen, 2004). On Marion Island, the species reproduces abundant wind-dispersed seeds all year round (Gremmen, 2004) and appears to be expanding its range (Ramaswiela *et al.*, in preparation).

***Cotula plumosa* Hook. f. (Asteraceae)**

On sub-Antarctic Marion Island, *C. plumosa* strictly dominates coastal lowland habitats (up to 100 m inland) enriched with nutrients and well exposed to frequent salt-spray (Huntley, 1970, 1971). Thus, this nitrophilic species dominates or co-occurs with *P. cookii* and *C. moschata* in Cotula/Coastal Herbfield vegetation on Marion Island. At coastal sites with active biotic activities of seals and seabirds *C. plumosa* together with *P. annua* may be important in plant succession processes (Gremmen, 1981). The reproductive phenology of this species is determined by both photoperiod and temperature (Huntley, 1970).

***Crassula moschata* Forst. f. (Crassulaceae)**

This succulent species is common in the Southern Hemisphere systems including on some sub-Antarctic islands (Dorne, 1977; Bywater & Wicken, 1984; Broughton & McAdam, 2005). On Marion Island, *C. moschata* occurs in coastal habitats characterised by fibrous, black or dark-brown peat and frequent wind-blown salt deposition (Huntley, 1970, 1971; Bywater & Wicken, 1984). These conditions are often met from sea-level to approximately 20 m in altitude (Huntley, 1970; le Roux & McGeoch, 2008a). Substantial increase in photoperiod and temperature during September drives the commencement of flowering activities of this plant on Marion Island (Huntley, 1970).

***Juncus effusus* L. (Juncaceae)**

*Juncus effusus* is a tuft-forming rush of about 1.5 m in height. The plant is indigenous to the Northern Hemisphere, and grows mostly on the edges of nutrient-rich wetlands or marshes (Smolders *et al.*, 2008), and frequently forms uniform stands through seedlings or rhizomes (Wetzel & Howe, 1999). In its native range, *J. effusus* photosynthesizes throughout the year, but during winter and autumn months the upper portions (tips) of its cylindrical leaves turn brown, a sign of little growth (Boyd, 1971; Mann & Wetzel, 1999). During spring, the plant reaches its highest point of productivity when new shoots emerge (Patton & Judd, 1988). On Marion Island this plant is restricted to four localities, and does not produce viable seeds (Gremmen, 2004).

***Montia fontana* L. (Portulacaceae)**

*Montia fontana* is a cosmopolitan species occurring, amongst other areas, on many sub-Antarctic islands, particularly in biotically nutrient-enriched coastal habitats. Quite often, in these habitats, *M. fontana* grows as typically dense, coprophilous mats. Moreover, the species may grow in other habitats quite a distance from the coast, up to 607 m a.s.l (Huntley, 1970; le Roux & McGeoch, 2008a). Relative to other vascular plant species in the sub-Antarctic region, this is apparently the species with the shortest growing season (Walton, 1982; Bergstrom *et al.*, 1997).

***Poa cookii* Hook. f. (Poaceae)**

This is a highly productive grass species common in biotically influenced habitats along the coast and close to sea-bird nests inland (Bate & Smith, 1983; Vidal *et al.*, 2003; Gremmen & Smith, 2008). In less nutrient-rich habitats the tussock rarely reaches its optimum growth, thus is often smaller. Like other grass species on Marion Island, *P. cookii* has an altitudinal limit of 659 m (Huntley, 1970; le Roux & McGeoch, 2008a). At low-altitude sites *P. cookii* flowers earlier in the



season (late August) (Huntley, 1970) thereby reaching its maximum reproductive biomass in February the following year (Smith, 1987, 1988). These activities are thought to be orchestrated by daylength on Marion Island (Huntley, 1970). The same way as the species produces shoots all year round, leaf senescence also occurs throughout the year (Bate & Smith, 1983; Vidal *et al.*, 2003). Due to slow decomposition rate on the island, litter accumulates and remains on the tussock for two seasons at most (Smith, 1987, 1988).

***Pringlea antiscorbutica* R. Br. (Brassicaceae)**

*Pringlea antiscorbutica* is endemic to the Kerguelen Biogeographic province, and on most of these islands it is a generalist species occurring across a wide range of habitats (Hennion & Walton, 1997; Chapuis *et al.*, 2000). For example, on Marion Island this species is widely distributed from the shoreline to approximately 500 m a.s.l (Huntley, 1970; le Roux & McGeoch, 2008a). The reproductive phenology of the Kerguelen cabbage, which commences in September, coincides with an increase in temperature and daylength on Marion Island (Huntley, 1970).

***Ranunculus biternatus* Sm. (Ranunculaceae)**

*Ranunculus biternatus* is a perennial, herbaceous plant indigenous to Southern Indian Ocean sub-Antarctic Islands, mostly in low-altitude, waterlogged habitats (Hennion & Walton, 1997). However, it has the ability and means to spread vegetatively. On Marion Island, this species has an altitudinal limit of 606 m (le Roux & McGeoch, 2008a). Its reproductive phenology is triggered by joint effects of daylength and temperature (Huntley, 1970).

***Rumex acetosella* L. (Polygonaceae)**

This plant is of European origin (Harris, 1970). It is an invader of the sub-Antarctic region and on many of the islands it is widely distributed (Wace & Dickson 1965; Walton & Smith, 1973; Carcaillet, 1993). However, on Marion Island the species is restricted to two, low altitude, nutrient-enriched sites. Currently, the species is not known to pose any threat to native vegetation on Marion Island, but over time this may change because it is now reproducing many more seeds than previously (Gremmen & Smith, 1999; Gremmen, 2004). Moreover, an area occupied by this species has expanded considerably and this may have resulted from its vigorous vegetative propagation (Gremmen, 2004). Elsewhere, the timing and period of flowering of this sorrel varies considerably with increasing altitude and latitude. However, its wind-pollinated flowering activity responds to daylength (Harris, 1970).

### ***Uncinia compacta* R. Br. (Cyperaceae)**

*Uncinia compacta* is a moisture- and temperature-sensitive sedge predominantly occurring on dry mires below 400 m a.s.l on Marion Island (Huntley 1970; le Roux & McGeoch, 2008a). This species produces seeds with hooks for animal-mediated dispersal (Hennion & Walton, 1997). A previous study has showed that it flowers approximately by early January (Huntley, 1970).

### **Sampling Design**

Sampling was conducted on the eastern side of sub-Antarctic Marion Island between May 2007 and April 2008. Five sites of 5 m x 5 m per species were identified randomly at low-altitude ranging from 8 to 180 m a.s.l (**Table 1**). For *A. selago*, ten cushions were identified and marked on a site without using the 5 m x 5 m plot design. Sites for a single species were selected such that they were separated by at least 500 m distance to avoid pseudo-replication. However, for *C. moschata* and *R. acetosella*, four and one site were used, respectively, either due to unavailability of more populations in the area under investigation or because sites of the same species were going to be < 500 m apart. For *J. effusus*, all four known populations were selected, but two of these were < 500 m apart. Some sampling sites supported more than one species. Sites were restricted to the eastern side of Marion Island to avoid the known intra-island variation in climate between the western and the eastern sides of the island (Nyakatyia & McGeoch, 2008). Similarly, sites had to be as close to the meteorological station as possible for accurate climate matching and comparison purposes (see next chapter). At each site, the coordinates (measured using a hand held Geographic Positioning System Unit, GARMIN e-trex), altitude, aspect, topography, moisture status and vegetation community were measured or recorded at the commencement and closing stages of the study (**Table 1**). For identification purposes, plots were marked using PVC pipes tagged with reflector tape.

### **Phenological Recording**

This study investigated phenology of plant species distributed across various functional groups namely: herbs, a shrub, grasses, a rush, a sedge; a cushion plant, and a fern. The studied species are representative of vascular plant functional groups that occur on Marion Island, most of which are widespread and common (see Gremmen & Smith, 2008; le Roux & McGeoch, 2008a). Herbaceous plants were measured using the same vegetative and reproductive measurements because they share most traits. Similarly, grasses, and the sedge and rush life forms were grouped together during census due to their morphological similarities. Plots were visited every 14 days from May 2007 to

April 2008 when all plants had already started dispersing seeds. However, during the winter months, heavy snow interfered with the sampling schedule thereby leading to a few sites that were not sampled (for fear of damaging the plants) or to sampling that was delayed by a few days. Of the 25 sampling weeks and 69 sites sampled, 46 different sites were affected at least once during the winter period.

During each site visit, the presence of apical leaf buds, leaf emergence, formed leaves, leaf senescence, flower set, blooming, pollen on flowers, fruit set, ripe fruit and dispersal events (see **Table 2** for phenophase definitions) were recorded on each of ten randomly selected individual plants for each of the species investigated, except for *A. selago* where ten cushions were continuously studied at each site. For *Ac. magellanica* and the graminoids (*Ag. magellanica*, *P. cookii*, *J. effusus* and *U. compacta*), a single branch and a rammet (tuft/tussock), respectively, were used as a representative of an individual plant. However, for the fern *B. penna-marina*, a randomly selected frond was regarded as individual plant for the purpose of this study. Given that some species like *M. fontana*, *C. plumosa*, *C. antarctica* and *C. mochasta* are carpet-forming and distinguishing an individual plant is not straight-forward, a 10 x 10 cm grid was used to represent a sampling unit (i.e. individual). Here, dominant leaf stages and all the reproductive phenophases observed within a grid were recorded to match with the data from species with identifiable individual plants, rammets or branches. It should also be noted that not every phenophase could be monitored on all species (see **Table 3**) because phenophases differ among species. Where necessary, a magnifying glass was used in the field for proper identification of phenophases and, in other instances, samples were taken to the laboratory for microscopic observation, more especially when a phenophase was observed for the first time on a species. For the sedge, *U. compacta*, of which the seeds are known to constitute an important component of the diet of house mice (Chown & Smith, 1993), two stainless steel, mice exclusion cages of 2 m<sup>3</sup> were placed at each site during the reproductive phase of the species' phenology. On *P. cookii* no cages were used and mice preyed on seeds immediately when they ripen, and this made the dispersal event difficult to monitor.

**Table 1:** Study site: locations and description

<b>Species</b>	<b>Site no.</b>	<b>Location</b>	<b>Vegetation type</b>	<b>GPS position</b>	<b>Altitude (m)</b>
<i>Ac. magellanica</i>	1	Path to Skua Ridge	<i>Acaena</i> Drainage Line	46°52.312'S, 37°50.847'E	67
	2	Banks of van den Boogaard River	Biotically Influenced Drainage Line	46°52.140'S, 37°51.365'E	24
	3	Path to Skua Ridge	<i>Acaena</i> Drainage Line	46°51.991'S, 37°51.075'E	41
	4	Junior's Kop	<i>Acaena</i> Drainage Line	46°52.834'S, 37°50.310'E	94
	5	Interior path to Ship's Cove	<i>Acaena</i> Drainage Line	46°51.664'S, 37°50.892'E	81
<i>Ag. magellanica</i>	1	Path to Skua Ridge	Mesic Mire Habitat	46°52.302'S, 37°50.747'E	73
	2	Trypot Beach	Mesic Mire Habitat	46°52.814'S, 37°51.766'E	30
	3	Path to Junior's Kop	<i>Agrostis</i> Grassland with rock clumps	46°52.668'S, 37°51.311'E	145
	4	Path to Junior's Kop	Mire Pool	46°52.617'S, 37°50.802'E	63
	5	Interior path to Ship's Cove	Wet Mire Habitat	46°52.035'S, 37°51.092'E	43
<i>A. selago</i>	1	Skua Ridge	Mesic Fellfield	46°52.092'S, 37°50.379'E	107
	2	Along van den Boogaard River	Mesic Fellfield	46°52.364'S, 37°50.061'E	98
	3	Path to Skua Ridge	Open Fernbrake	46°52.290'S, 37°50.719'E	70

	4	Coastal Route to Trypot Beach	Coastal Salt-spray	46°52.731'S, 37°51.922'E	26
	5	Path to Junior's Kop	Open Fernbrake	46°52.707'S, 37°51.218'E	47
<i>B. penna-marina</i>	1	Coastal route to Ship's Cove	Closed Fernbrake	46°52.235'S, 37°51.387'E	20
	2	Trypot Beach	<i>Blechnum</i> Slope/Closed Fernbrake	46°53.032'S, 37°51.957'E	28
	3	Path to Junior's Kop	Open Fernbrake	46°52.699'S, 37°51.145'E	53
	4	Junior's Kop	Open Fernbrake	46°52.815'S, 37°50.223'E	114
	5	Along van den Boogaard River	Closed Fernbrake	46°52.365'S, 37°50.038'E	95
<i>C. antarctica</i>	1	Close to Gentoo Lake	Biotic Grassland	46°52.691'S, 37°51.77'E	28
	2	Trypot Beach	Biotic Influenced	46°53.035'S, 37°52.140'E	14
	3	Coastal route to Ship's Cove	Biotic Pool Complex	46°51.826'S, 37°51.358'E	18
	4	Ships' Cove	Biotic Lawn	46°51.29'S, 37°50.605'E	33
	5	Coastal route to Ship's	Biotic Lawn and Pool	46°52.203'S, 37°51.397'E	21
<i>C. fontanum</i>	1	Trypot Beach	Open Fernbrake	46°52.993'S, 37°52.018'E	24
	2	Banks of van den Boogaard River	Riparian	46°52.260'S, 37°50.294'E	76

	3	Close to the Dam	Slope Crest	46°52.546'S, 37°49.769'E	145
	4	Banks of van den Boogaard River	Human Disturbed habitat	46°52.438'S, 37°49.933'E	100
	5	Way to Waterfall	<i>Acaena</i> Drainage Line	46°52.920'S, 37°49.181'E	180
<hr/>					
<i>C. plumosa</i>	1	Ship's Cove	Biotically influenced slope with bird burrows	46°51.145'S, 37°50.353'E	48
	2	Trypot Beach	Biotically influenced slope with bird burrows	46°53.006'S, 37°52.071'E	41
	3	Coastal route to Ship's Cove	Coastal Herbfield	46°52.136'S, 37°51.519'E	21
	4	Coastal route to Ship's Cove	Biotic Herbfield	46°51.823'S, 37°51.343'E	20
	5	Trypot Beach	Biotically Influenced	46°52.722'S, 37°51.818'E	20
<hr/>					
<i>C. moschata</i>	1	Coastal route to Trypot Beach	Coastal Salt-spray	46°52.765'S, 37°51.987'E	13
	2	Coastal route to Ship's Cove	Coastal Salt-spray	46°52.117'S, 37°51.579'E	8
	3	Coastal route to Ship's Cove	Coastal Salt-spray	46°51.837'S, 37°51.455'E	16
	4	Coastal route to Ship's Cove	Coastal Salt-spray	46°52.419'S, 37°51.462'E	14
<hr/>					
<i>J. effusus</i>	1	Trypot Beach	Biotically Influenced	46°53.040'S, 37°52.151'E	12
	2	Along van den Boogaard River	Closed Fernbrake and a bit of Drainage Line	46°52.203'S, 37°51.283'E	10

	3	Ship's Cove	Edge <i>Blechnum</i> Mire and <i>Blechnum</i> Slope Fernbrake	46°51.132'S, 37°50.367'E	40
	4	Ship's Cove	Cotula Herbfield	46°51.142'S, 37°50.563'E	36
<i>M. fontana</i>	1	Close to Gentoo Lake	Disturbed Coastal Grassland	46°52.684'S, 37°51.775'E	19
	2	Trypot Beach	Mire Pool	46°53.034'S, 37°52.104'E	20
	3	Coastal route to Ship's	Biotic Pool	46°52.13'S, 37°51.481'E	11
	4	Ship's Cove	Biotic Mud	46°51.279'S, 37°50.579'E	37
	5	Coastal route to Ship's Cove	Biotic Pool	46°51.828'S, 37°51.364'E	12
<i>P. cookii</i>	1	Path to Skua Ridge	<i>Acaena</i> Drainage Line	46°52.312'S, 37°50.847'E	67
	2	Trypot Beach	Open Fernbrake	46°52.996'S, 37°52.014'E	23
	3	Coastal route to Ship's Cove	Biotic Open Fernbrake	46°52.151'S, 37°51.382'E	30
	4	Path to Junior's Kop	Slope Crest	46°52.528'S, 37°51.047'E	46
	5	Junior's Kop	Open Fernbrake	46°52.815'S, 37°50.223'E	114
<i>P. antiscorbutica</i>	1	Junior's Kop	<i>Acaena</i> Drainage Line	46°52.752'S, 37°50.03'E	138
	2	Ship's Cove	Open Fernbrake/slope crest	46°51.448'S, 37°50.635'E	70

	3	Ship's Cove	Open Fernbrake/slope crest	46°51.151'S, 37°50.34'E	51
	4	Coastal route to Ship's Cove	<i>Acaena</i> Drainage Line invaded by <i>A. stolonifera</i>	46°52.417'S, 37°51.439'E	11
	5	Skua Ridge	Open Fernbrake	46°52.272'S, 37°50.02'E	106
<hr/>					
<i>R. biternatus</i>	1	Close to Gentoo Lake	Biotic Mire	46°52.694'S, 37°51.755'E	29
	2	Banks of van den Boogaard River	Mire Pool	46°52.19'S, 37°51.38'E	13
	3	Coastal route to Ship's Cove	Mire Pool	46°51.826'S, 37°51.311'E	11
	4	Ship's Cove	Mire Pool	46°51.279'S, 37°50.579'E	37
	5	Banks of van den Boogaard River	Mire Pool	46°52.187'S, 37°51.133'E	43
<hr/>					
<i>R. acetosella</i>	1	Close to Gentoo Lake	Biotically Influenced	46°52.657'S, 37°51.66'E	11
<hr/>					
<i>U. compacta</i>	1	Trypot Beach	Mesic Mire	46°52.766'S, 37°51.656'E	28
	2	Coastal route to Ship's Cove	Slope crest	46°52.245'S, 37°51.365'E	28
	3	Coastal route to Ship's Cove	Slope crest	46°52.007'S, 37°51.539'E	19
	4	Path to Skua Ridge	Dry Mire	46°52.688'S, 37°51.216'E	48
	5	Ship's Cove	Salt-spray <i>Cotula-Azorella</i>	46°51.117'S, 37°50.434'E	46
<hr/>					



**Table 2 (A-D):** Definition of vegetative and reproductive phenology for each growth form**A. Herbs and shrub**

<i>Vegetative phenophases</i>	<i>Description</i>
Apical forming leaf bud	Just formed, young and closed buds
Apical leaf emergence	Bursting/opening leaf buds
Apical fully formed leaves	Large sized and fully open leaves
Apical leaf senescence	Standing dying or dead leaves; yellow or brownish coloured
<i>Reproductive phenophases</i>	<i>Description</i>
Flower buds set	Recently appeared flower bud and are normally small and green with no stalk; when fully formed become large, coloured and sometimes stalk appears
Flowering	Bursting flower buds; recently open and fully open flowers/inflorescences (full-bloom with petals visible)
Pollen release	Pollen grains on paper/cotton after tapping; matured or dry anther
Fruit set	Recently formed fruit after pollination; normally small and green; small seed heads
Ripe fruit	Larger fruits mostly coloured, harder or starting to dry-out; when touched ripe seeds easily fall-off
Seed dispersal	Open seed sac; seeds on the ground close to the parent plant; seeds stick and remain on the cloth; fruits susceptible to touch

**B. Graminoids**

<i>Vegetative phenophases</i>	<i>Description</i>
1. Old/brown leaves	Standing dying/senesced leaves attached to the plant
2. New green shoots	Small green leaves that are often folded or in-rolled
3. New green leaves	These leaves are larger and longer than shoots with open tips
4. Developed green leaves	These are fully open, large and green leaves
<i>Reproductive phenophase</i>	<i>Description</i>
1. Inflorescence set	Appearing inflorescence from leaf sheath and is often green
2. Flowering	Inflorescence with pollen grains after tapping or from observations. On <i>J. effusus</i> developed inflorescences were used.
3. Fruit set	Fattening of the inflorescence; soft seeds felt after touching
4. Ripe fruits	Larger, harder, open sac and colour changes
5. Seed dispersal	Missing seeds on inflorescence; seed heads stick on the glove

**C. Cushion**

<i>Vegetative phenophases</i>	<i>Description</i>
Green leaves	These are percentages of all green leaves on the cushion be they emerging or developed leaves

Autumnal senescence	These are leaves starting to go brown or already brown
<i>Reproductive phenophases</i>	<i>Description</i>
Flower buds	Emerging light-green features and are often larger when fully developed
Flowering	Opening flower buds to fully open flowers with anthers
Pollen release	Drying out or matured anthers
Fruit set	Small, green fruits immediately after anther desiccation
Ripe fruit	Fruits bulges and become harder and turns brown or reddish
Seed dispersal	Loose seeds on top of the cushion or when the number of fruits on the cushion is reduced

#### D. Fern

<i>Vegetative phenophases</i>	<i>Description</i>
Forming fronds	Small & largely curled frond dominated by red colour
Emerging fronds	Less curled frond with red & green colours
Fully formed fronds	Large, green & fully open fronds
Fronds senescence	Brown fronds or fronds with grey blotches

**Table 3:** Observed phenophases on each species

Species	Vegetative phenology				Reproductive phenology					
	Leaf buds	Leaf emergence	Formed leaves	Leaf senescence	Flower set	Flowering or bloom	Pollen release	Fruit set	Ripe fruits	Seed dispersal
<i>Ac. magellanica</i>	√	√	√	√	√	√	√	√	X	√
<i>Ag. magellanica</i>	√	√	√	√	√	√	√	√	X	√
<i>A. selago</i>	√	√	√	√	√	√	√	√	√	√
<i>B. penma-marina</i>	√	√	√	√	X	X	X	X	X	X
<i>C. antarctica</i>	√	√	√	√	√	√	√	√	√	√
<i>C. fontanum</i>	√	√	√	√	√	√	√	√	√	√
<i>C. plumosa</i>	√	√	√	√	√	√	√	√	X	√
<i>C. moschata</i>	√	√	√	√	√	√	√	√	√	√
<i>J. effusus</i>	√	√	√	√	√	√	X	X	X	X
<i>M. fontana</i>	√	√	√	√	√	√	√	√	√	√
<i>P. cookii</i>	√	√	√	√	√	√	√	√	√	X
<i>P. antiscorbutica</i>	√	√	√	√	√	√	√	√	√	√
<i>R. acetosella</i>	√	√	√	√	√	√	√	√	√	√
<i>U. compacta</i>	√	√	√	√	√	√	√	√	√	√

## DATA ANALYSIS

To analyse the plant phenology data, sampling dates (calendar dates) were converted into Julian dates, with 1<sup>st</sup> of January being the 1<sup>st</sup> Julian day and 1<sup>st</sup> of February the 32<sup>nd</sup> Julian day and so on. After analysis, these dates were converted back to normal calendar dates for data display. Species phenophases were grouped into major stages i.e. growth and developmental stages (Vegetative and reproductive phenology).

### *Vegetative phenology*

In determining the growth phenology, the number of plants in each growth stage (leaf budding, leaf emergence, formed leaves and senescencing leaves) was quantified at each site during a visit. The number of plants in each stage at each site for each species was then used to calculate the mean ( $\pm$  standard deviation) stage for each species during each sampling event. These means were then used to show the species growth phenology over a full growing season. The individual species sampling event date was determined by averaging (mean) the dates in which sites of the species were visited and sampled (because not every site was visited on the same day during each 14 day sampling event – typically each species was documented over its c. five sites over the course of 3-4 days). For the graminoids, the total number of leaves in each category (i.e. fully formed leaves, shoots, new green and brown leaves) was quantified across all ten sampled plants (tufts/rammet) at a site. After having calculated the total number of all leaves from all sampled plants irrespective of the stage, the proportion of each leaf stage (percentage) was determined at a site-level. Each leaf stage proportion from sites of the species was then averaged to obtain the species' mean leaf proportions during each sampling event. The proportions were used in analysing the graminoids growth phenology because sampled tufts/rammets/tussocks may not necessarily be an individual plant. For the cushion plant, *A. selago*, the percentage of cushion area covered with brown or green leaves was quantified and a mean was calculated across all ten sampled cushions for each site. Then the mean percentage of either brown or green leaves at site-level was used to calculate the grand mean percentage during every sampling event. Calculating the proportions of green leaves (buds and matured) to brown leaves (senesced & discoloured) on each cushion was the most accurate way of measuring growth phenology for this species. Finally, vegetative phenology of all species was plotted as column graphs with standard deviations except in the case of *R. acetosella*, where only one site was used. Thus the sample size is  $n = 5$  for all species except for *C. moschata* ( $n = 4$ ), *J. effusus* ( $n=4$ ) and *R. acetosella* ( $n=1$ ).

### ***Reproductive phenology***

To determine the first occurrence dates of events on focal species, the Julian day in which at least a single plant/branch/rammet at a site of the species was observed with any reproductive phenophase was regarded as the onset date of that particular event at a site-level. A mean (and standard deviation) of the phenophase first emergence dates from sites of the species was then calculated to determine the species, mean phenophase onset date (as opposed to the first onset date). The time/duration of each phenophase was quantified by counting the number of sampling events (weeks) when at least one plant at a site was observed in the given phenophase (see **Table 2**). Each sampling event denoted two weeks duration since phenological observations were undertaken fortnightly. A mean (and standard deviation) for this period was calculated using each site as an independent data point. The mean onset date and the mean duration of each phenophase were then plotted together, as suggested by Post *et al.* (2008). The peak occurrence dates of events were calculated as the date on which the number of sampled individuals with flower buds (young and mature), flowers (and pollen release), fruits (ripe and unripe) or dispersing seeds was the greatest (maximum) at each site. The peak dates of a particular event across sites were then averaged (mean) to determine the peak occurrence date of a species. To investigate any significance differences in timing, peak occurrence date and duration of events between species Generalised Linear Models (GLZ) (Poisson Distribution, Log-link function, corrected for overdispersion where required) were used as implemented in Statistica v.9.0 (Statsoft, Tulsa, Oklahoma). The 95 % confidence intervals of the GLZ weighted means were then used to group the species into homogenous sets of those with early, late, or intermediate onsets, and with variation in duration and peak timing. The 95% confidence interval overlaps were also used to assess whether the alien and indigenous species showed any consistent differences in these traits. In addition, the groups were also examined using a one-way ANOVA, Tukey post hoc test, even though the data typically had heterogeneous variances and so violated one of the assumptions of analysis of variance.

## **RESULTS**

### ***Vegetative phenology***

Vegetative growth occurred throughout the year in all of the focal species except for *A. selago* and *Ac. magellanica*, which showed some seasonality (**Fig. 1**). For example, between June and early September *Ac. magellanica* had already shed all of its developed leaves, but young leaves continued to form and emerge from the branches (**Fig. 10**). Some of these young or emerging leaves also

senesced before they matured in the winter months. During late autumn and winter months (May to August) more than 60 % of *A. selago* cushion surface area was covered with brown leaves and this only changed from mid-September to late March the following year (**Fig. 1A**). By April, when the study ceased, the proportion of brown leaves was larger than that of green ones. In these two species the timing of increased growth immediately followed development. On other species leaf bud formation, leaf emergence, developed leaves and subsequently senesced leaves were observed throughout the year with no major peak occurrences (**Fig. 1**).

#### *Timing/ first occurrence date and duration of reproductive events*

The first plant species observed with flower buds on Marion Island was *C. fontanum* on 8<sup>th</sup> May at the commencement of the study, and the last species, *J. effusus*, lagged behind by months setting buds in summer (**Fig. 2**). However, the onset of flower buds occurred in spring in most species. *Pringlea antiscorbutica* and *P. cookii* were the first two species to mark the beginning of spring season by setting buds in mid-September. Generally, the largest number of species had their flower buds peak date in the summer months except for *P. antiscorbutica*, *P. cookii* and *Ac. magellanica*, which peaked in spring (**Table 4**). The flower bud duration ranged from 3.6 weeks on *R. biternatus* to 40.4 weeks on *C. fontanum*; with a mean of 13 weeks across all species (**Fig. 2**).

*Cerastium fontanum* was the only species observed with flowers in autumn (May). However, in most species flowering began in spring and continued through the summer months, when the last plant flowered on 19<sup>th</sup> January (**Fig. 2**). The peak production of flowers on most species occurred during the summer months, ranging from 1<sup>st</sup> December to 16<sup>th</sup> February, with the exception of *Ac. magellanica*, *A. selago* and *P. antiscorbutica* which peaked by late November (**Table 4**). *Cerastium fontanum*, which initiated flowering in autumn, showed the longest flowering duration (32 weeks) while *A. selago* flowered for least number of weeks (3.6 weeks) (**Fig. 2**). With the exception of *C. fontanum* where pollen release was first observed in summer (2<sup>nd</sup> January) while flowers were spotted months earlier in autumn at the commencement of the study, the timing of pollen coincided with full-bloom activity on most species or at least occurred within a short interval (**Fig. 2**). The longest period in which pollen was observed on flowers was 12.5 weeks for *C. moschata*. Neither pollen nor fruits were observed in the case of *J. effusus*.

*Pringlea antiscorbutica* was the first species observed with fruits in spring, but the majority of the species only initiated fruiting activity in summer particularly between 3<sup>rd</sup> December and 5<sup>th</sup>

February (**Fig. 2**). By the end of January 69.2% of the species had already reached their peak fruiting date (**Table 4**). The formation and development of these fruits continued for 11.6 weeks in *Ag. magellanica* to 32 weeks in *R. acetosella* and had a mean of 16.5 weeks, a substantially longer period compared with budding and flowering event durations (**Fig. 2**). The time required for fruit maturation/ripening (the difference between fruit set date and ripe fruits) also differed with species, ranging from 2.8 days in *M. fontana* to 56 days in *P. antiscorbutica*. On the 20<sup>th</sup> December, *Ac. magellanica* started to disperse seeds, long before any other species (**Fig. 2**). Except for *Ag. magellanica* and *C. moschata*, which started dispersing their seeds in early autumn (March), seed dispersal stage for the rest of the species began in summer and peaked mostly between January and February (**Table 4**). *Rumex acetosella* dispersed its fruits for the longest duration (26 weeks) relative to other species (**Fig. 2**). On *P. cookii*, mice cut down the inflorescence immediately when the seeds had ripened and thus dispersal phenology could not be determined.

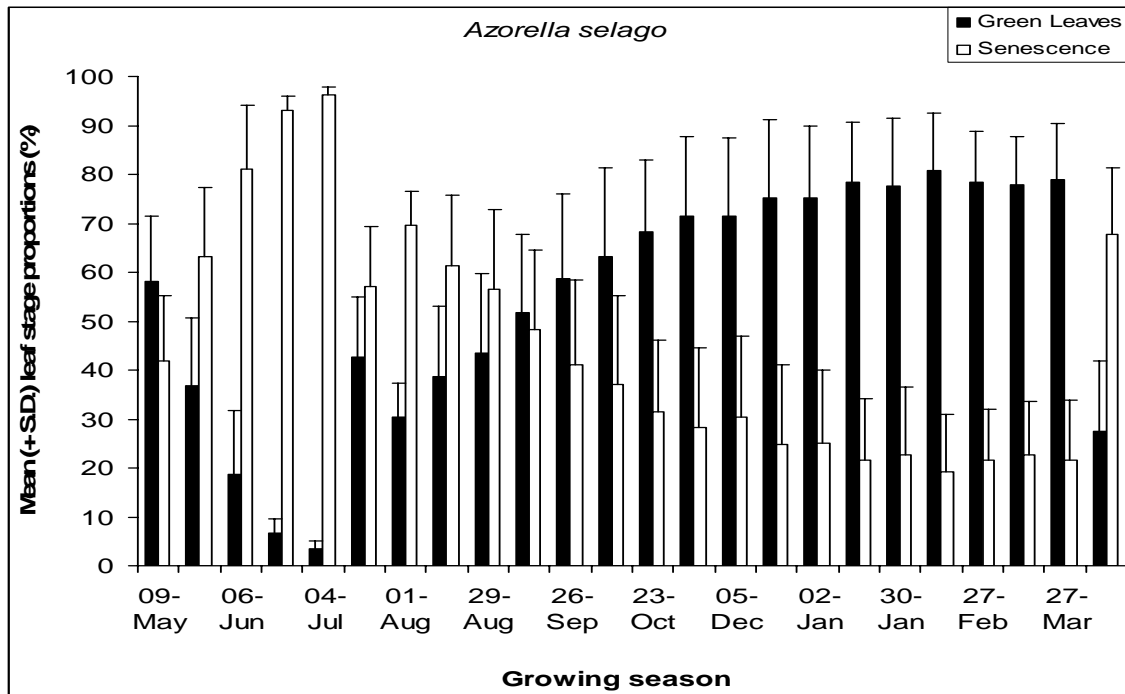
### ***Species comparison***

The timing of flower buds, flowering, fruit set, ripe fruit and seed dispersal varied considerably among the species (**Fig. 3**). Three homogenous sets of species was observed, the early (*C. fontanum*, *P. antiscorbutica*, *P. cookii*, *Ac. magellanica*, *A. selago*), intermediate (*C. plumosa*, *C. antarctica*, *R. acetosella*, *U. compacta*, *R. biternatus*, *C. moschata* and *M. fontana*) and late (*Ag. magellanica* and *J. effusus*) budding species (**Fig. 3A**). Most of the species that set flower buds early, intermediate or late in the season followed the same pattern in flowering except for *C. plumosa* and *C. antarctica* which moved from the intermediate group to the early one (**Fig. 3B**). However, the majority of species overlapped greatly on their timing of pollen release, fruit set and fruit ripening events (**Fig. 3C-E**); consequently no single grouping could be identified. During the dispersal stage *Ac. magellanica*, *M. fontana*, *C. plumosa*, and *R. biternatus* dispersed early, while *C. fontanum*, *A. selago*, *U. compacta*, *C. antarctica*, *P. antiscorbutica* and *R. acetosella* concluded their life-cycle stages in the transition between early and late dispersing species (**Fig. 3F**). Finally, *Ag. magellanica* and *C. moschata* dispersed their seed the latest. The mean duration of each phenophase (budding, flowering, pollen release, fruiting and dispersal) also differed amongst species (**Fig. 4**). However, there were no major identifiable homogenous species groups. This was true also of the alien and indigenous species, which could not be readily separated from the rest of the species. The peak occurrence dates of phenophases (flower buds, flowering, fruiting and seed dispersal), similar to their respective first occurrence date, varied considerably with species (**Fig. 5**).

However, their phenophase peak occurrence dates of each species occurred almost in an unbroken progression or continuum over months resulting in much overlap amongst species.

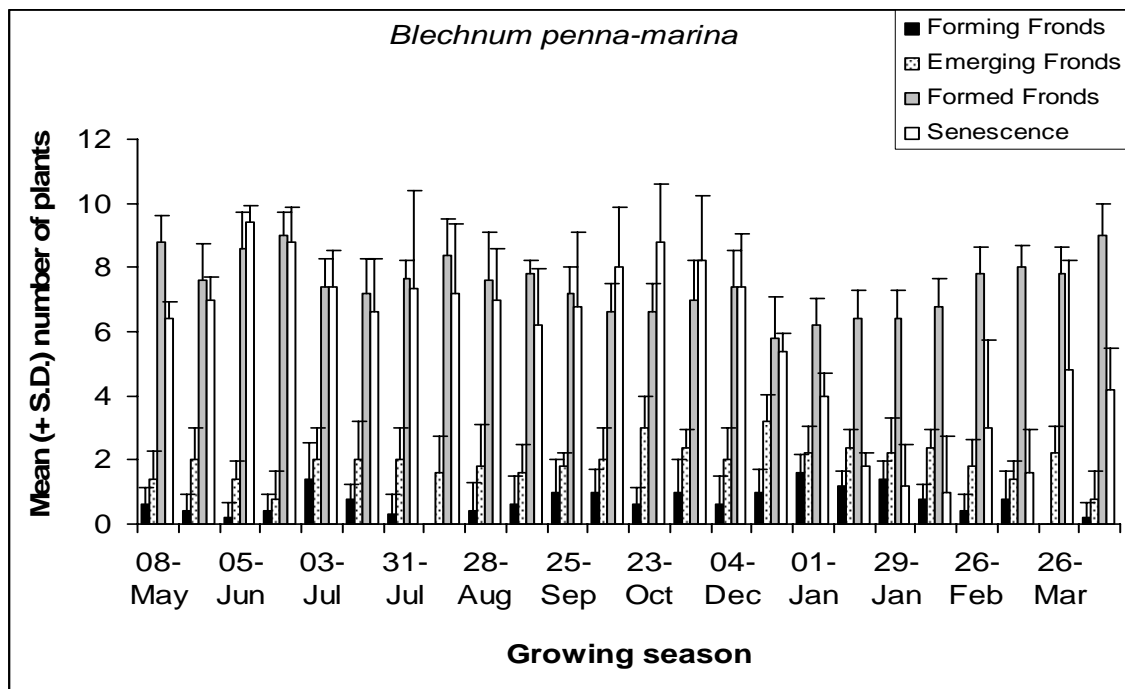
## Cushion Plant

A)



## Fern

B)

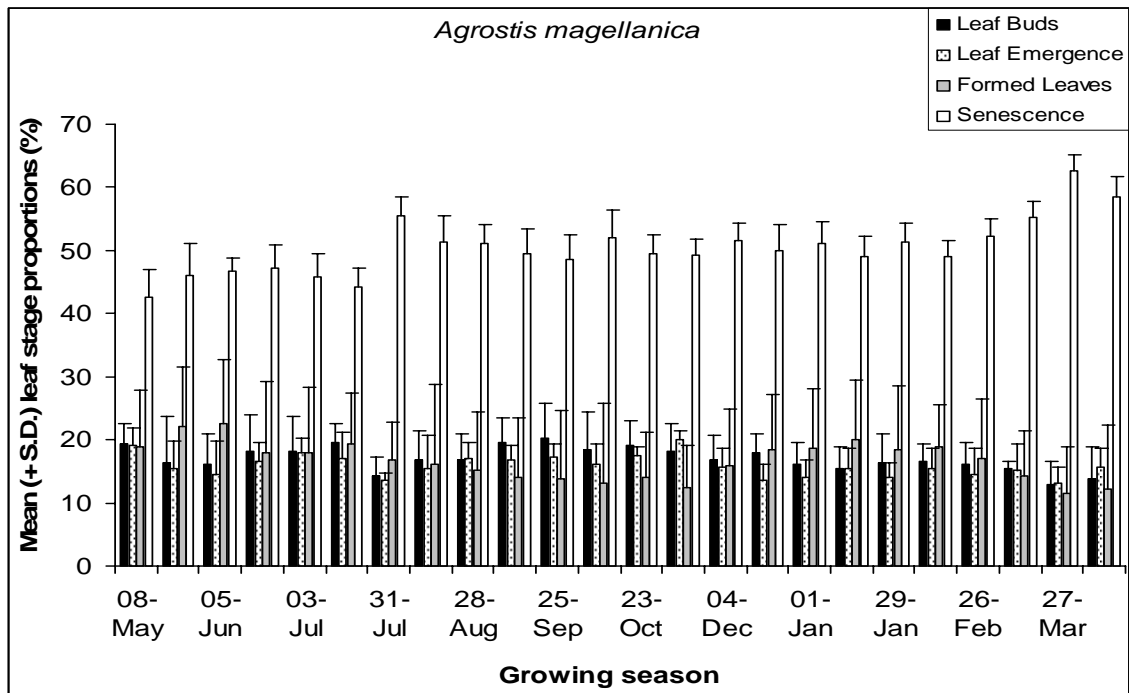


**Fig. 1 (A & B):** Phenology of vegetative growth of: A) *A. selago*, and B) *B. penna-marina*. Bars indicate mean values and the error bars indicate the standard deviation. X-axis denotes the mean sample dates for each species.

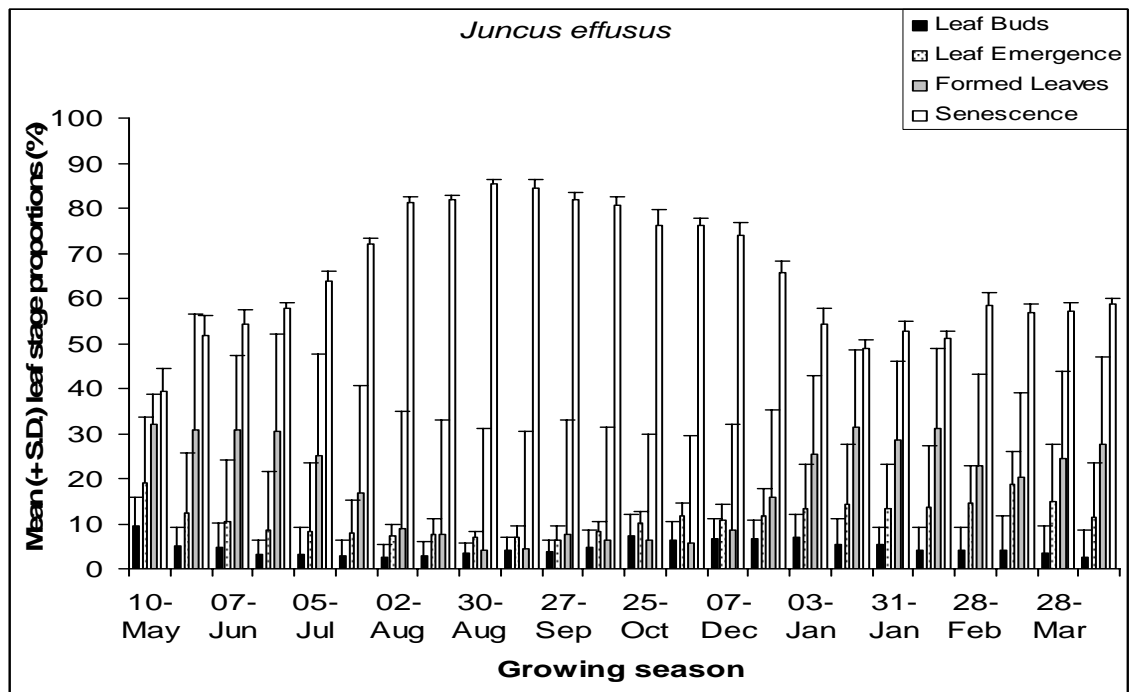


## Graminoids

C)



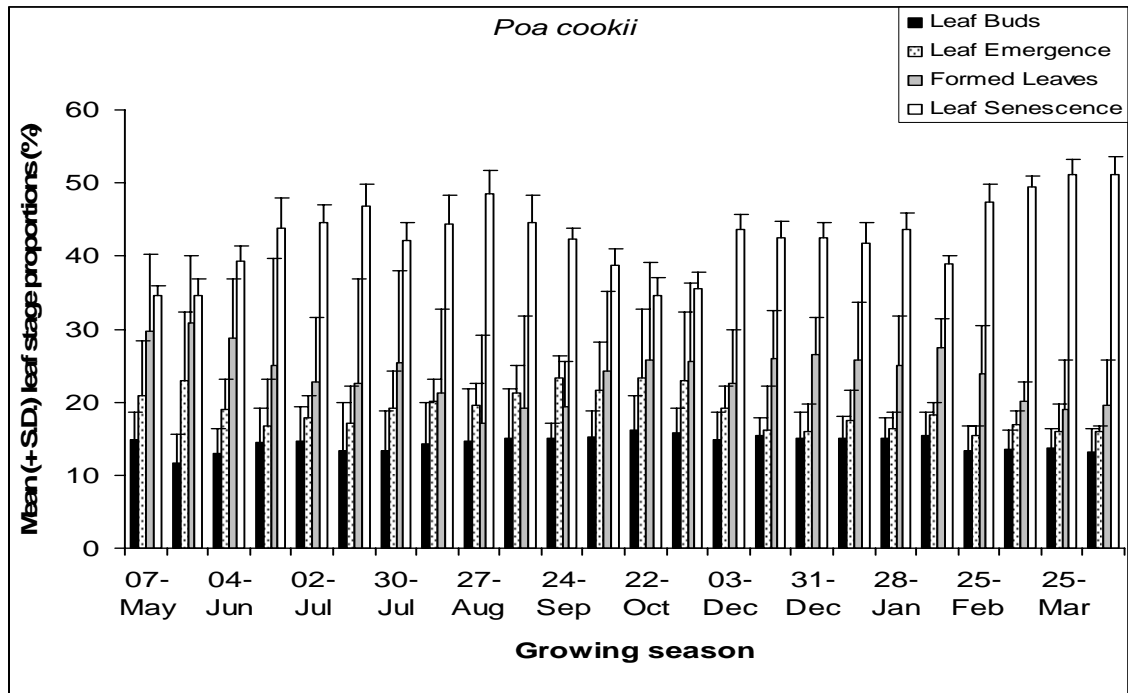
D)



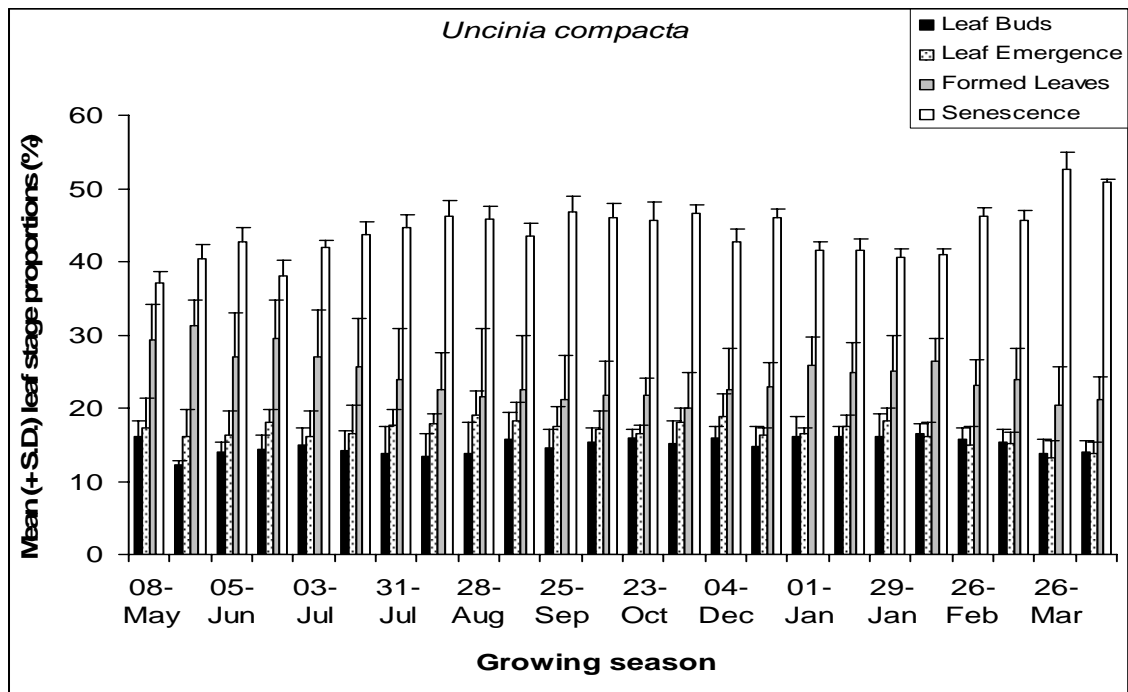
**Fig. 1 (C & D):** Phenology of vegetative growth of: C) *Ag. magellanica*, and D) *J. effusus*. Bars indicate mean values and the error bars indicate the standard deviation. X-axis denotes the mean sample dates for each species.

## Graminoids

E)



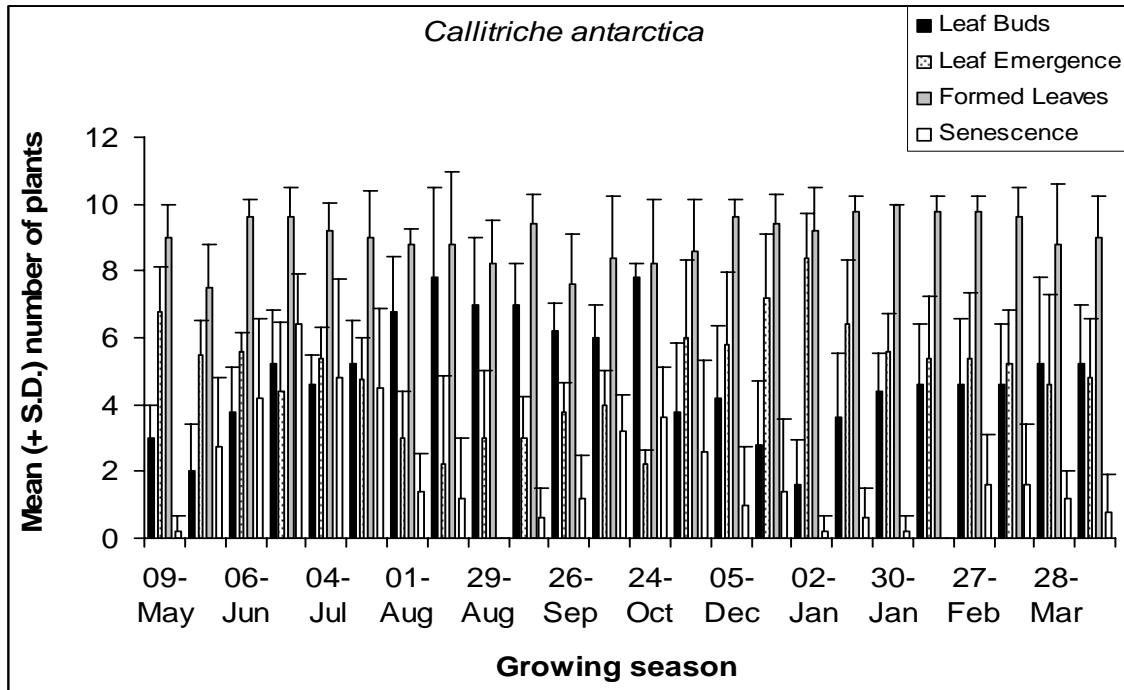
F)



**Fig. 1 (E & F):** Phenology of vegetative growth of: E) *P. cookii* and, F) *U. compacta*. Bars indicate mean values and the error bars indicate the standard deviation. X-axis denotes the mean sample dates for each species.

Herbs

G)



H)

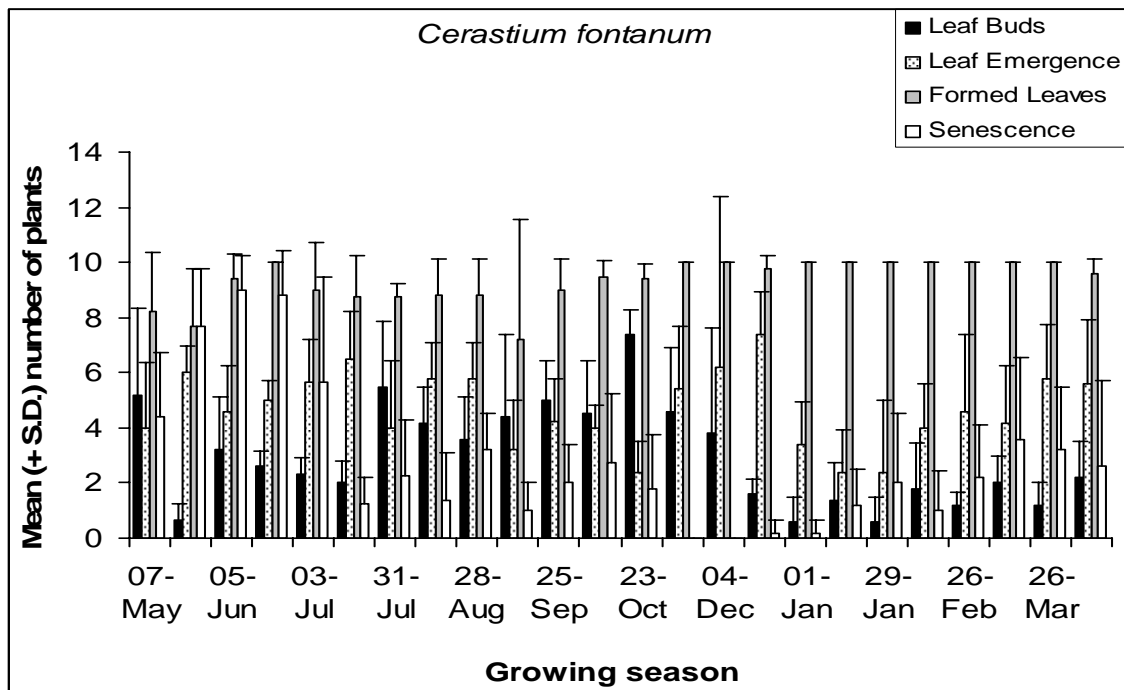
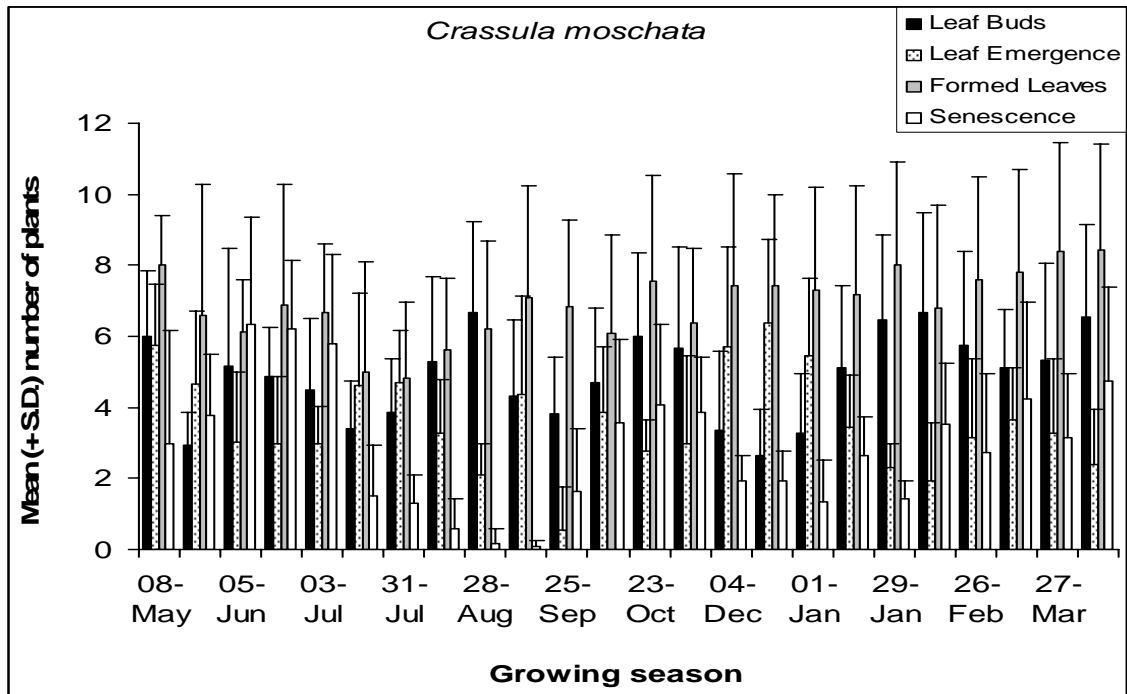


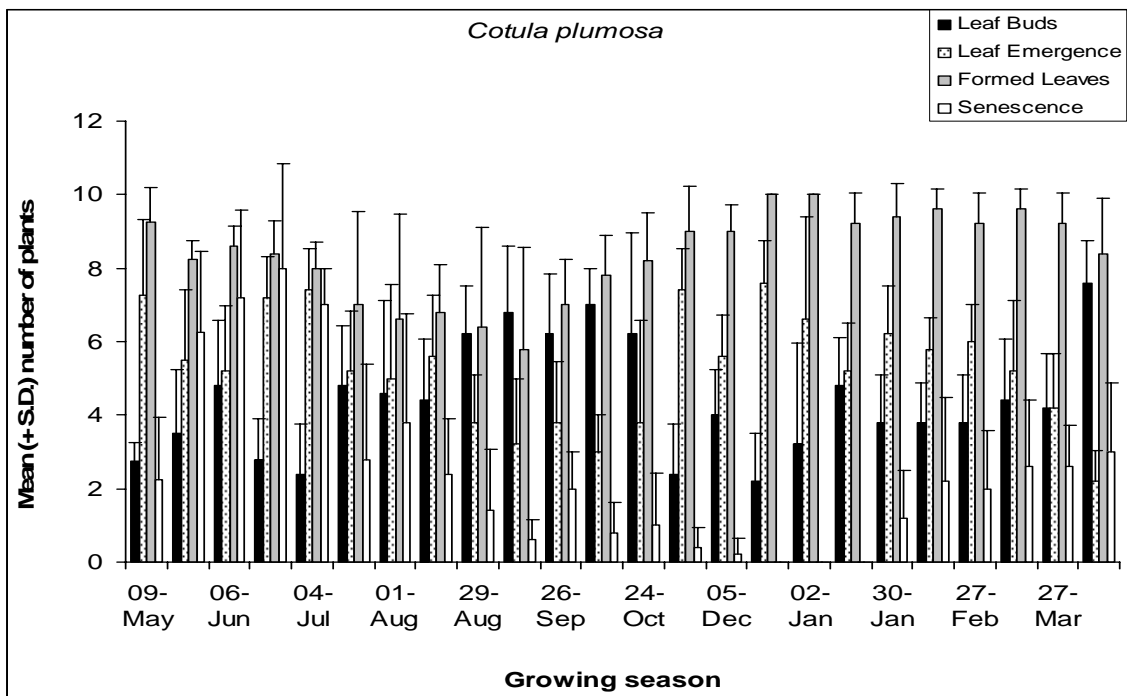
Fig. 1 (G & H): Phenology of vegetative growth of: G) *C. antarctica* and, H) *C. fontanum*. Bars indicate mean values and the error bars indicate the standard deviation. X-axis denotes the mean sample dates for each species.

## Herbs

I)



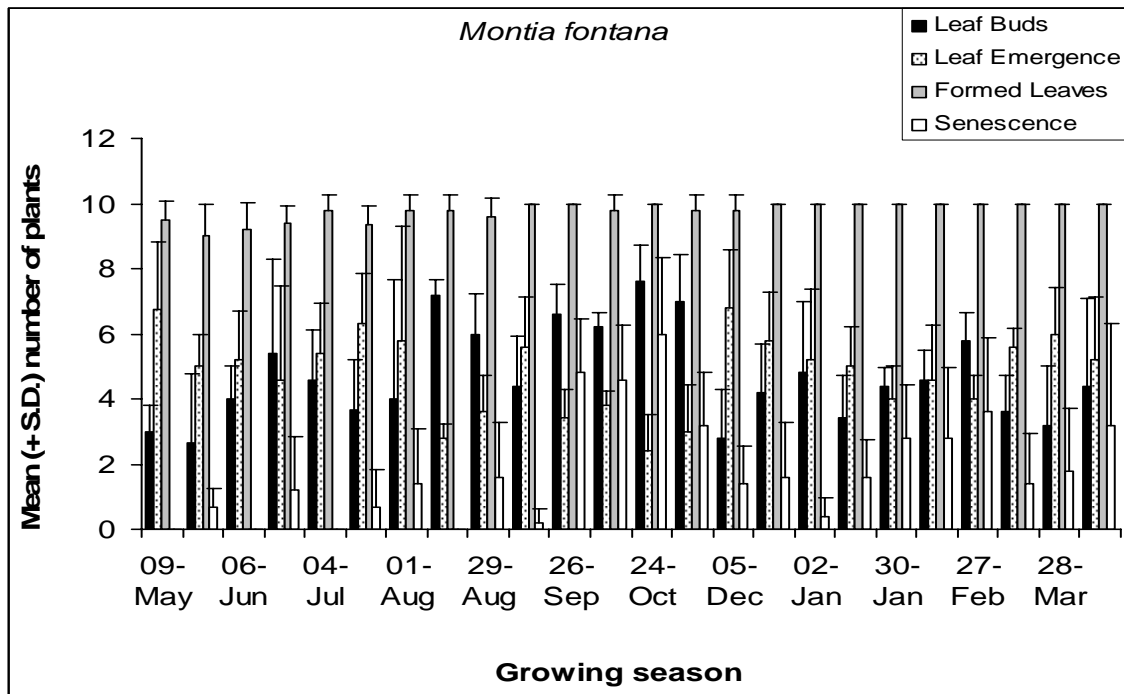
J)



**Fig. 1 (I & J):** Phenology of vegetative growth of: I) *C. moschata* and, J) *C. plumosa*. Bars indicate mean values and the error bars indicate the standard deviation. X-axis denotes the mean sample dates for each species.

Herbs

K)



L)

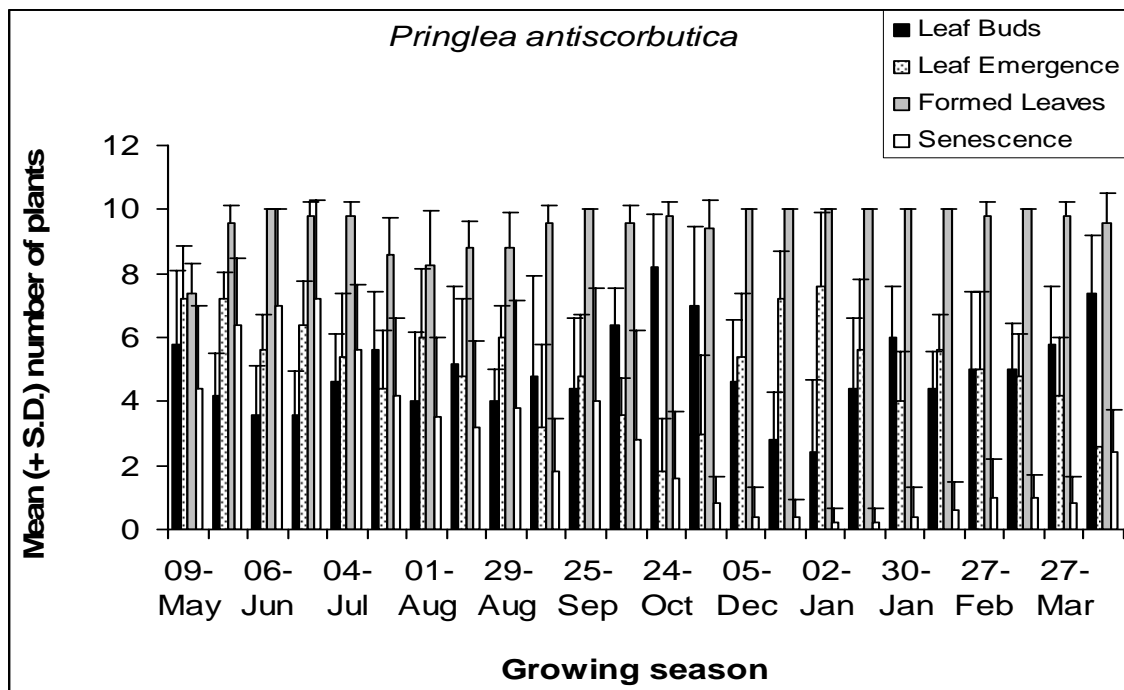
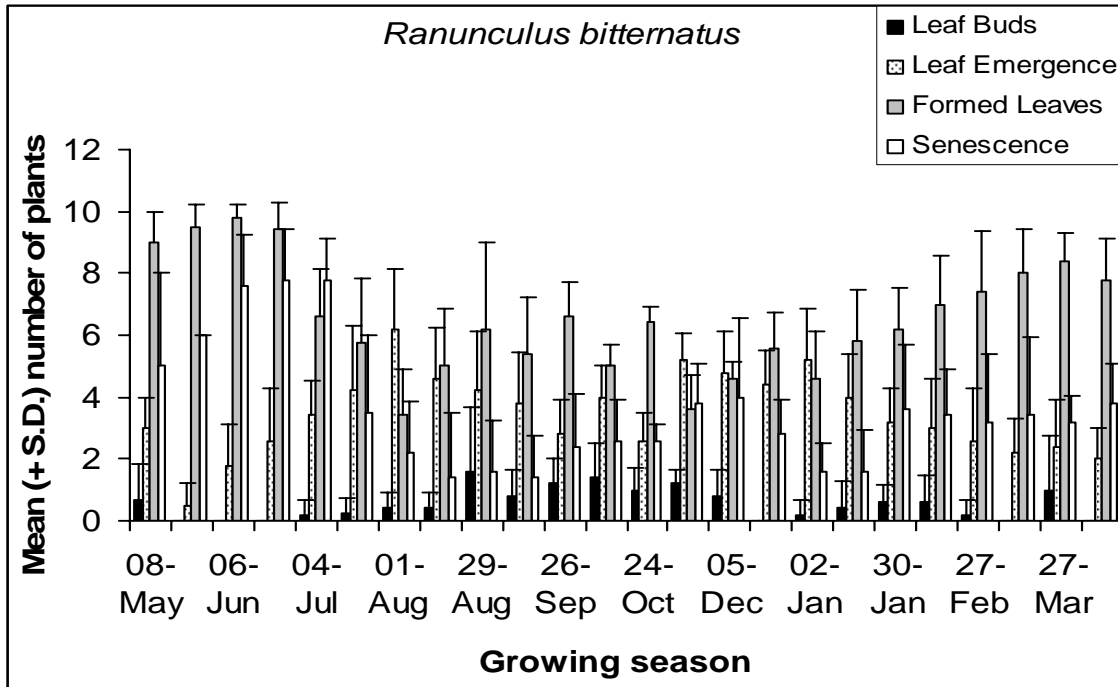


Fig. 1 (K & L): Phenology of vegetative growth of: K) *M. fontana* and, L) *P. antiscorbutica*. Bars indicate mean values and the error bars indicate the standard deviation. X-axis denotes the mean sample dates for each species.

Herbs

M)



N)

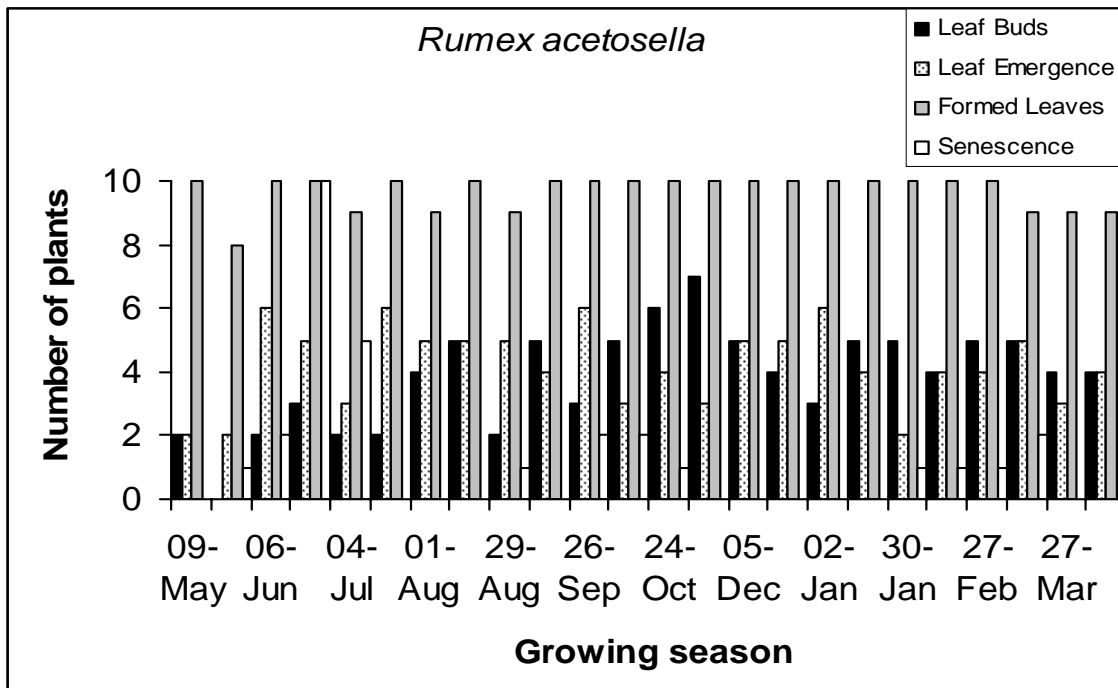
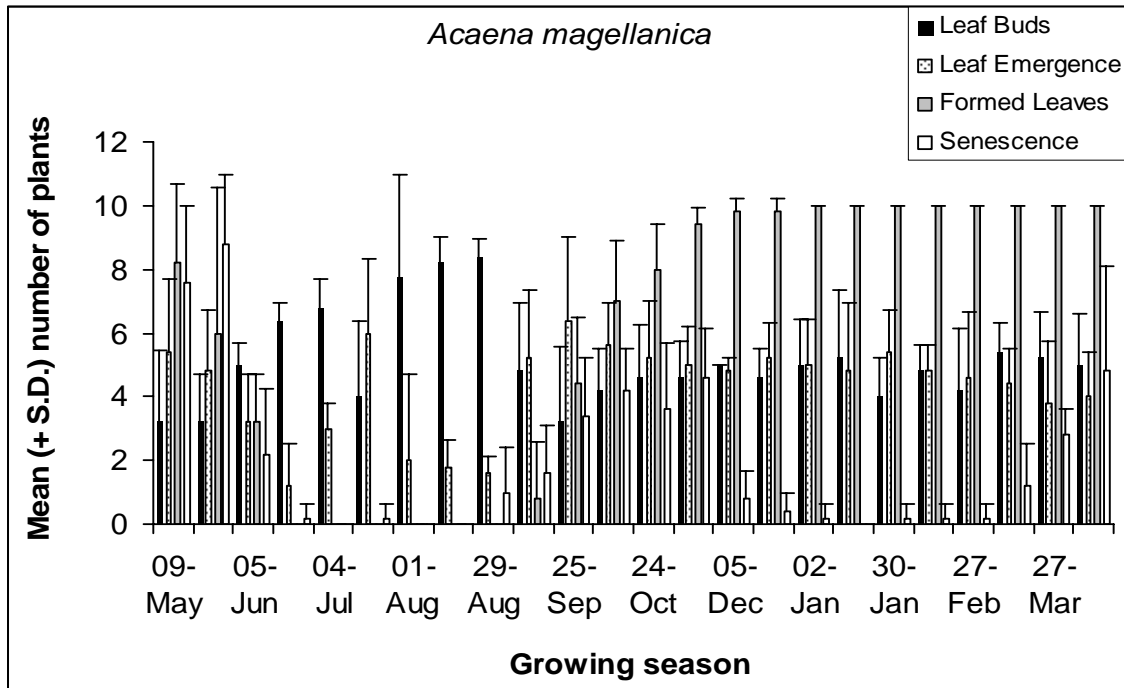


Fig. 1 (M & N): Phenology of vegetative growth of: M) *R. biternatus* and, N) *R. acetosella*. Bars indicate mean values and the error bars indicate the standard deviation. For *R. acetosella* there are no error bars because one site was sampled. X-axis denotes the mean sample dates for each species.

**Shrub**

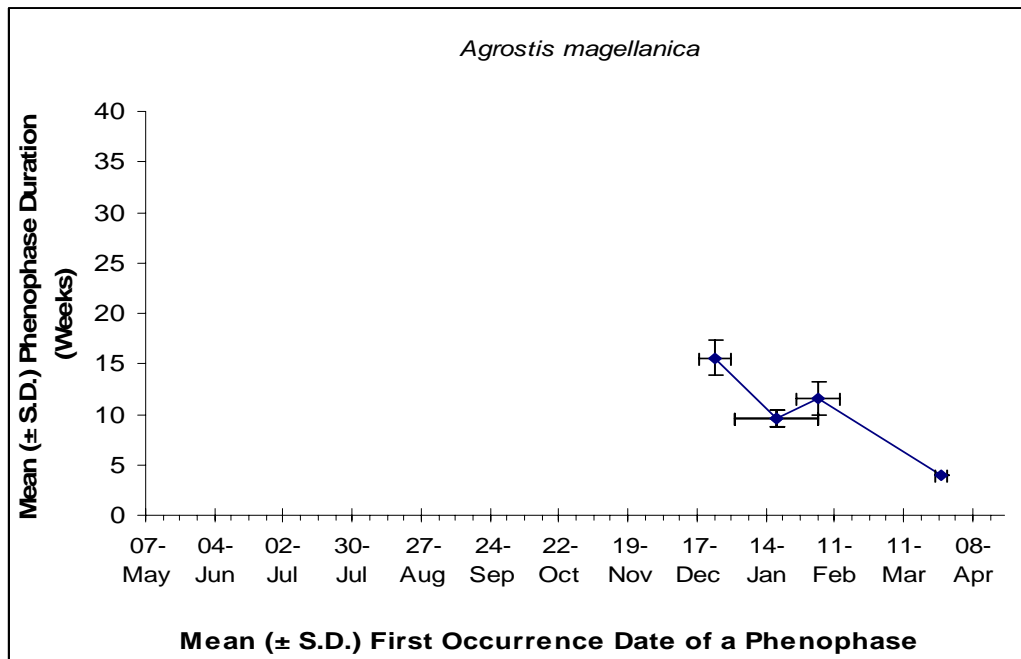
O)



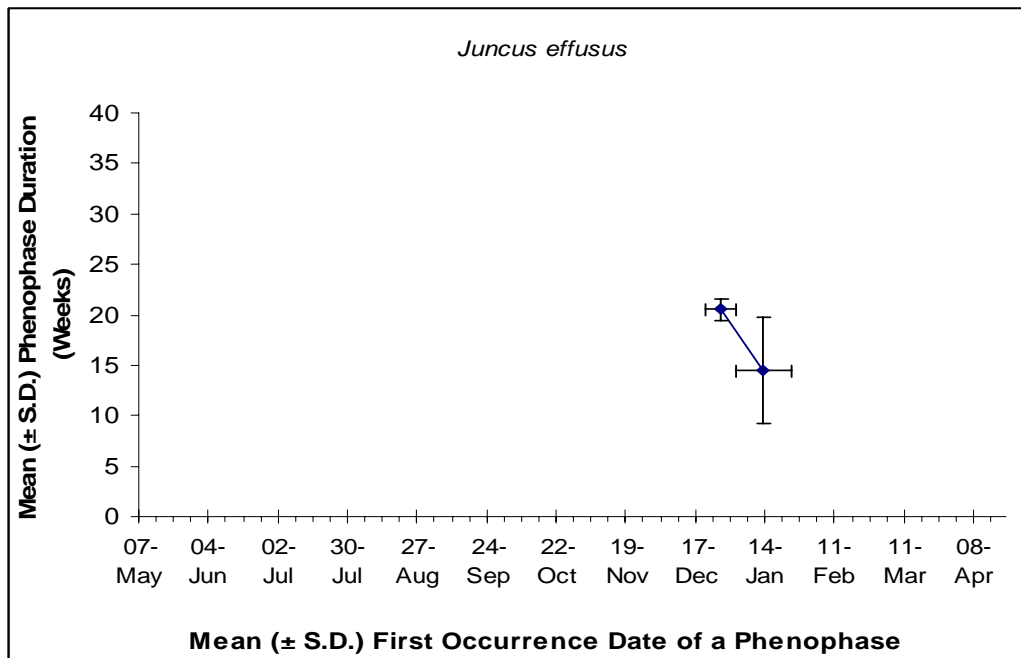
**Fig. 1 (O):** Phenology of vegetative growth of O) *Ac. magellanica*. Bars indicate mean values and the error bars indicate the standard deviation. X-axis denotes the mean sample dates for each species.

## Graminoids

A)



B)

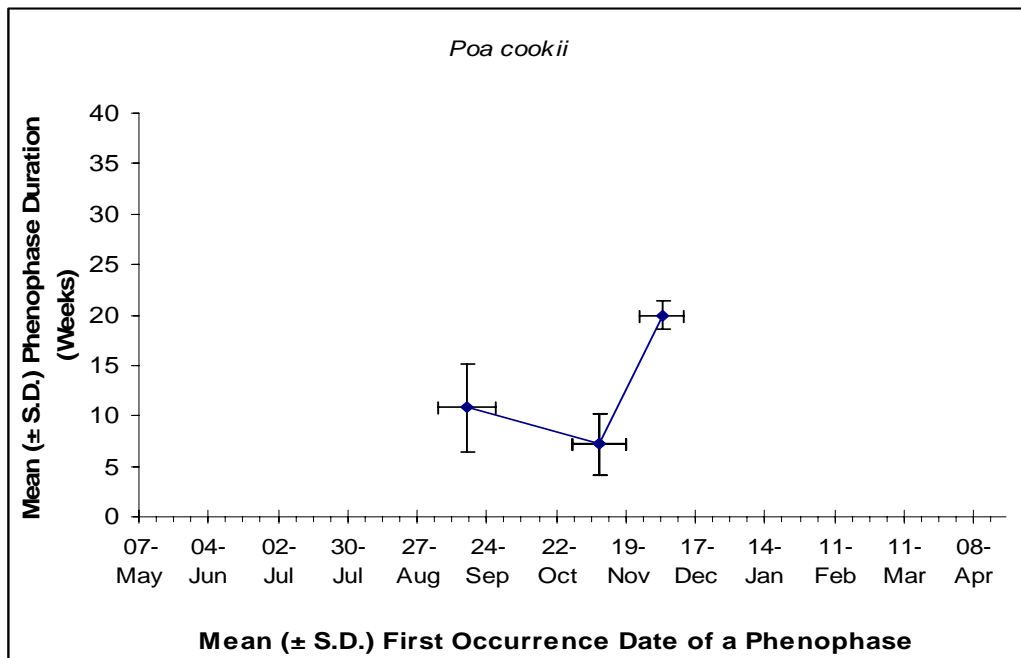


**Fig. 2 (A & B):** Developmental phenology of A) *Ag. magellanica* and, B) *J. effusus*. Each dot represents mean phenophase timing and duration in sequential order of occurrence from flower buds, flowering (and pollen release), fruiting to seed dispersal. Error bars indicate the standard deviation.

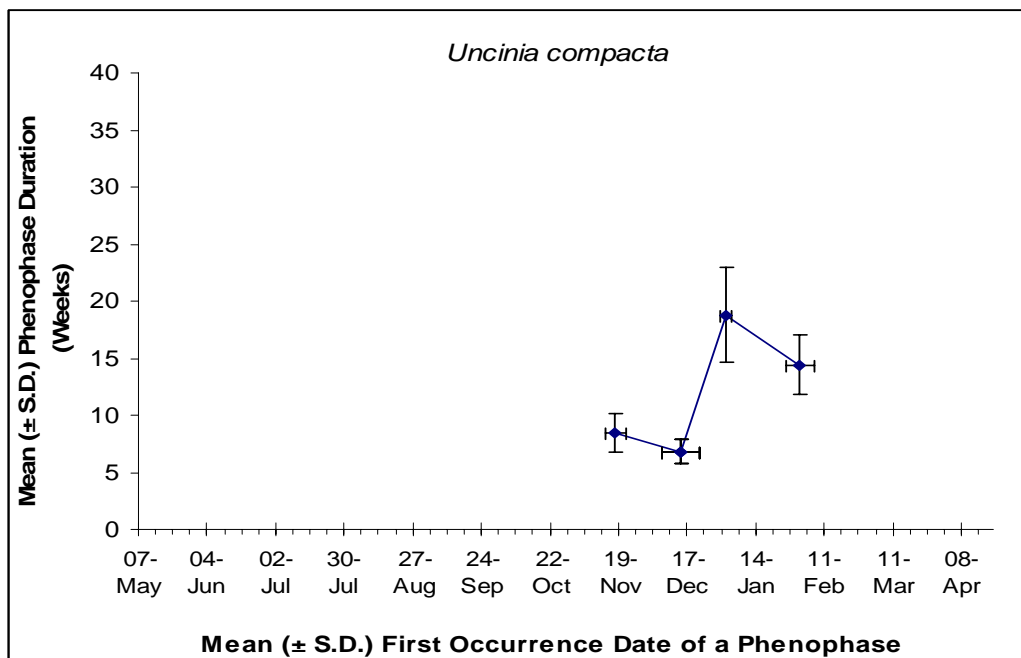


## Graminoids

C)



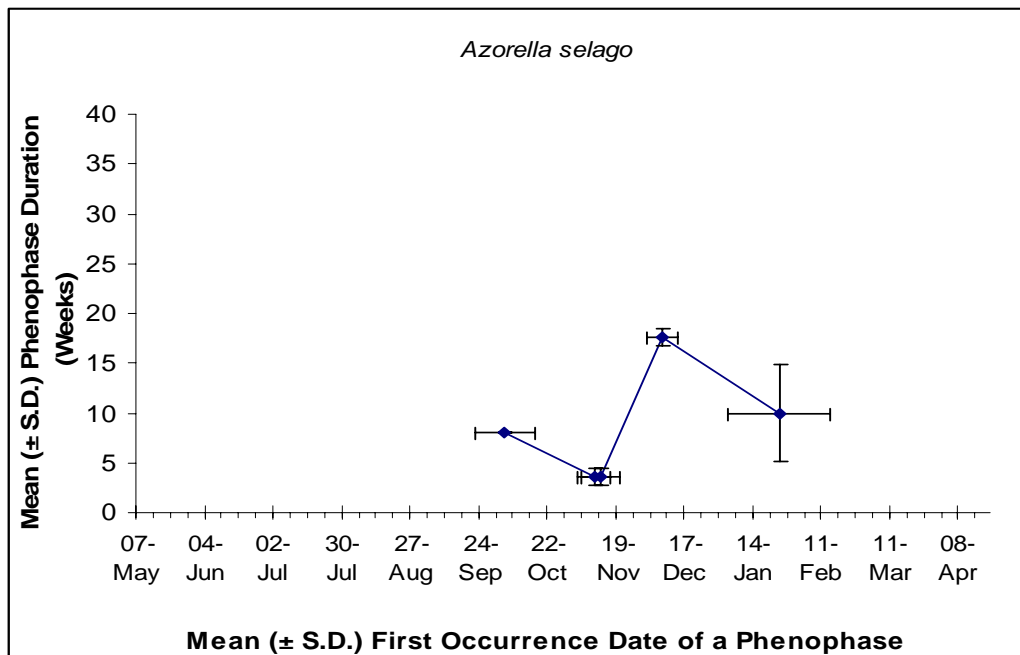
D)



**Fig. 2 (C & D):** Developmental phenology of C) *P. cookii*, and D) *U. compacta*. Each dot represents mean phenophase timing and duration in sequential order of occurrence from flower buds, flowering (and pollen release), fruiting to seed dispersal. The error bars indicate the standard deviation.

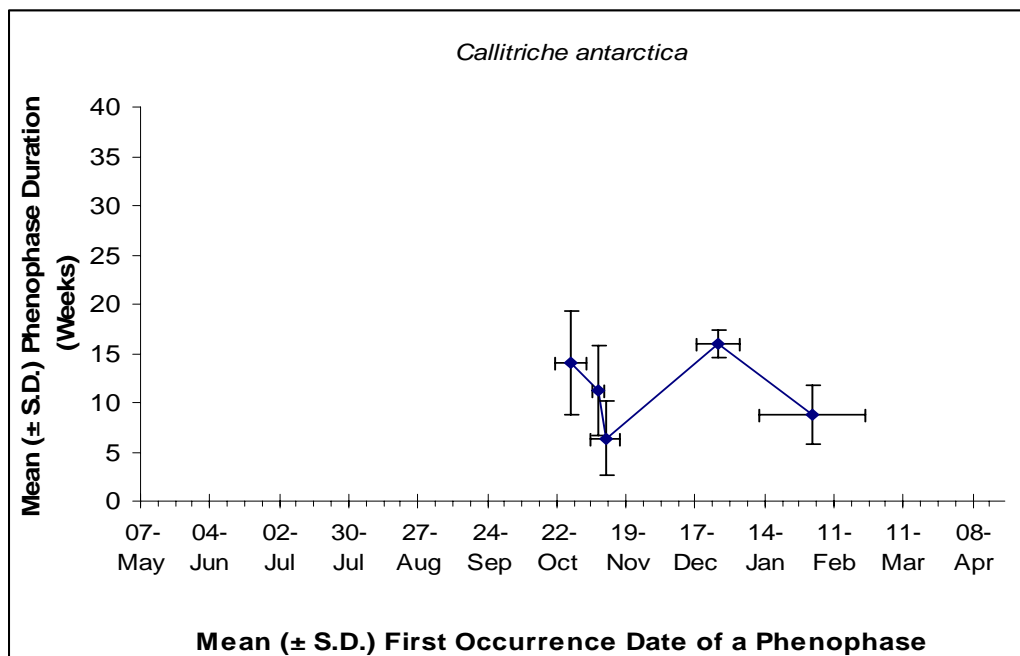
## Cushion Plant

E)



## Herb

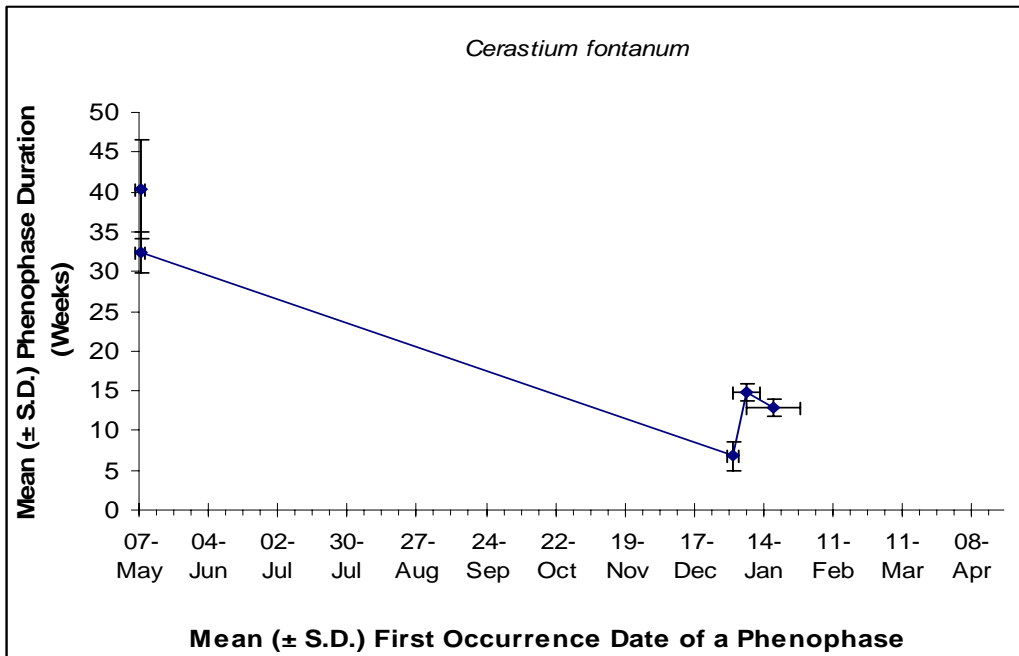
F)



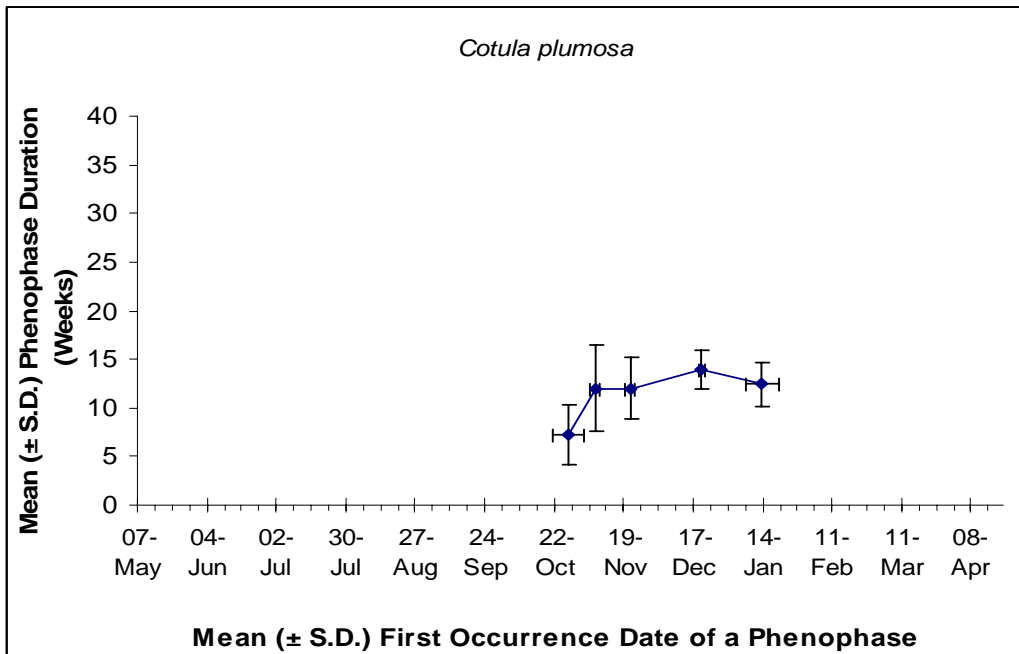
**Fig. 2 (E & F):** Developmental phenology of E) *A. selago* and, F) *C. antarctica*. Each dot represents mean phenophase timing and duration in sequential order of occurrence from flower buds, flowering, pollen release, fruiting to seed dispersal. The error bars indicate the standard deviation.

## Herbs

G)



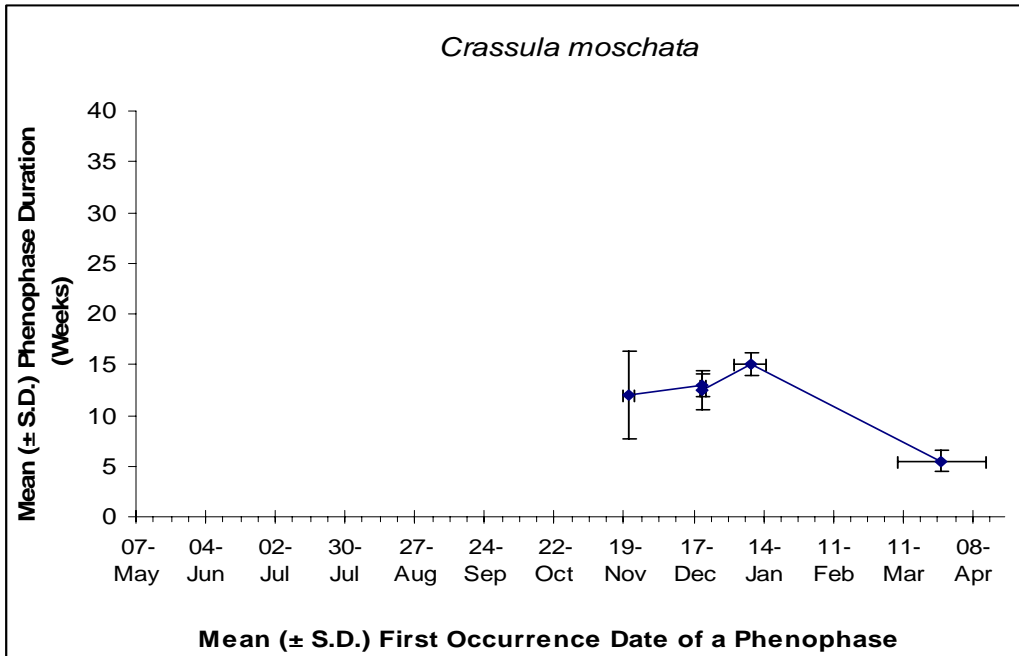
H)



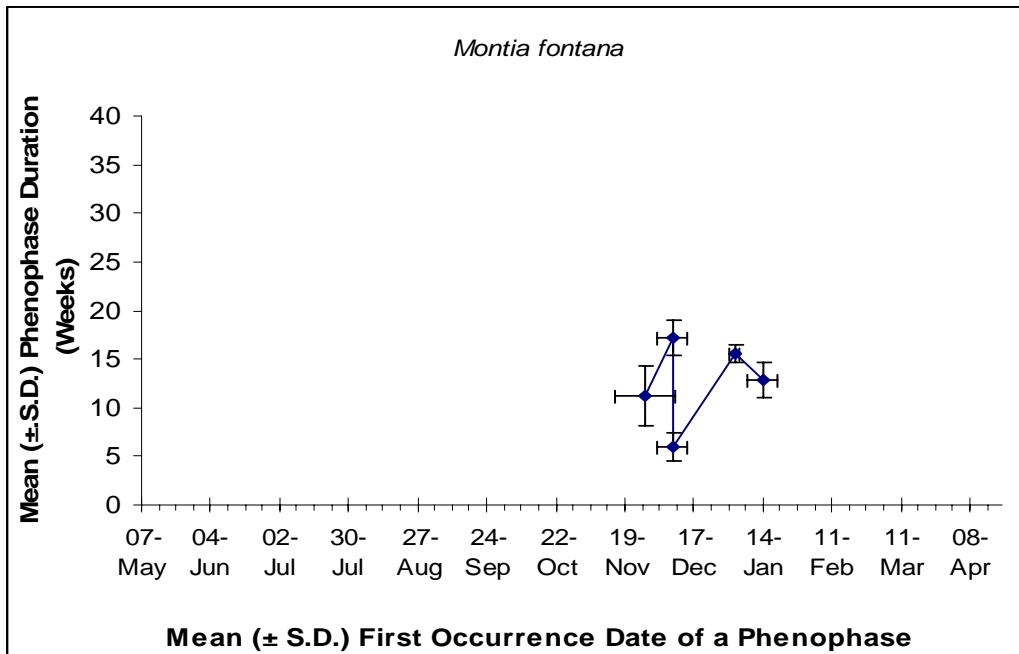
**Fig. 2 (G & H):** Developmental phenology of G) *C. fontanum* and H) *C. plumosa*. Each dot represents mean phenophase timing and duration in sequential order of occurrence from flower buds, flowering, pollen release, fruiting to seed dispersal. The error bars indicate the standard deviation.

## Herbs

I)



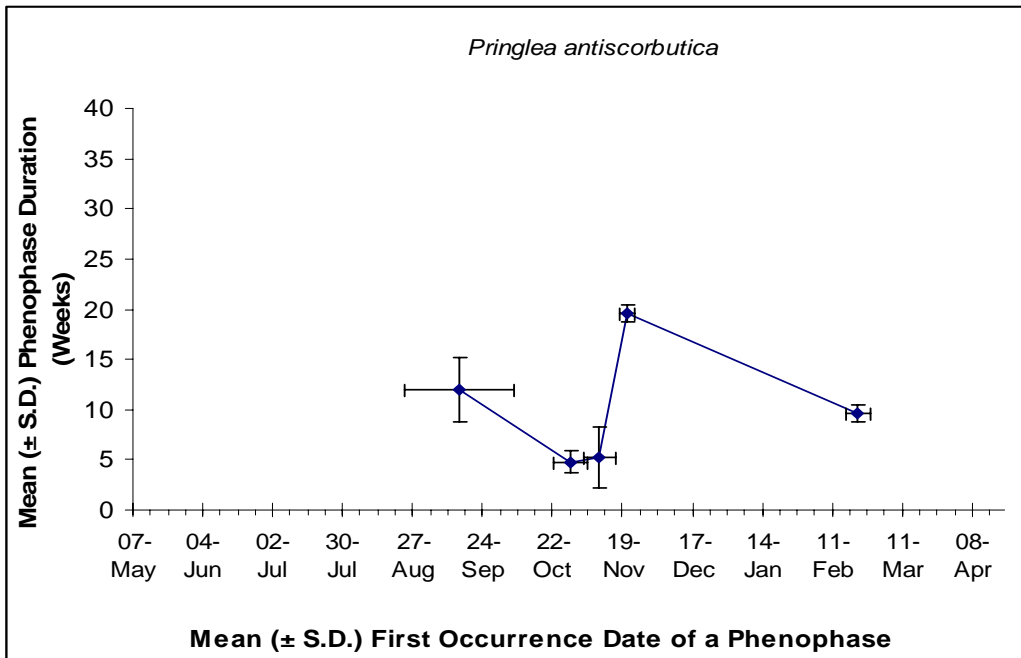
J)



**Fig. 2 (I & J):** Developmental phenology of I) *C. moschata* and J) *M. fontana*. Each dot represents mean phenophase timing and duration in sequential order of occurrence from flower buds, flowering, pollen release, fruiting to seed dispersal. The error bars indicate the standard deviation.

Herbs

K)



L)

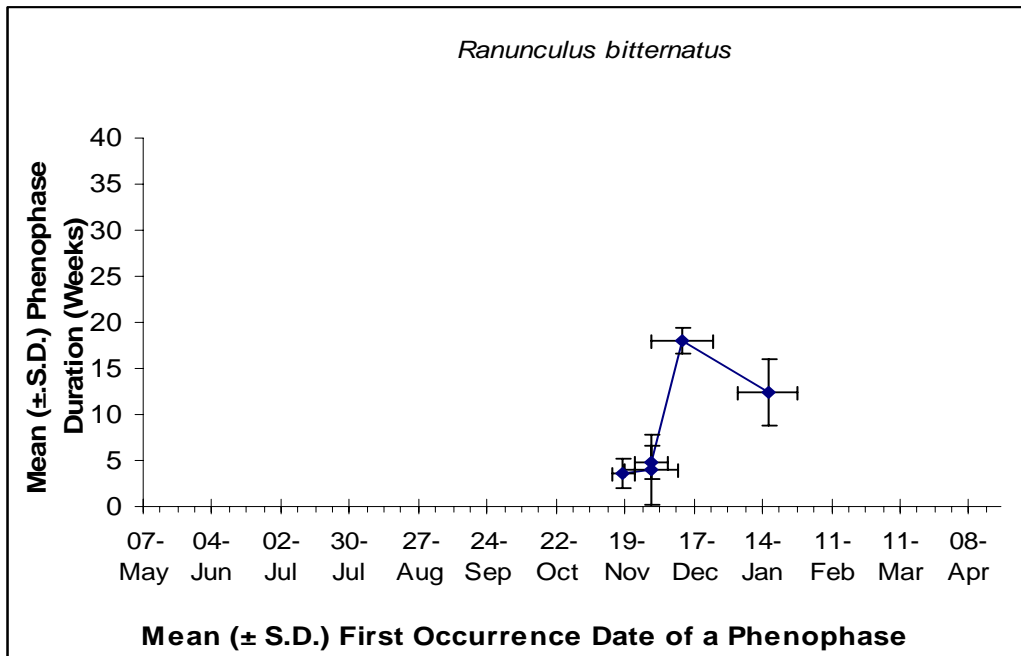
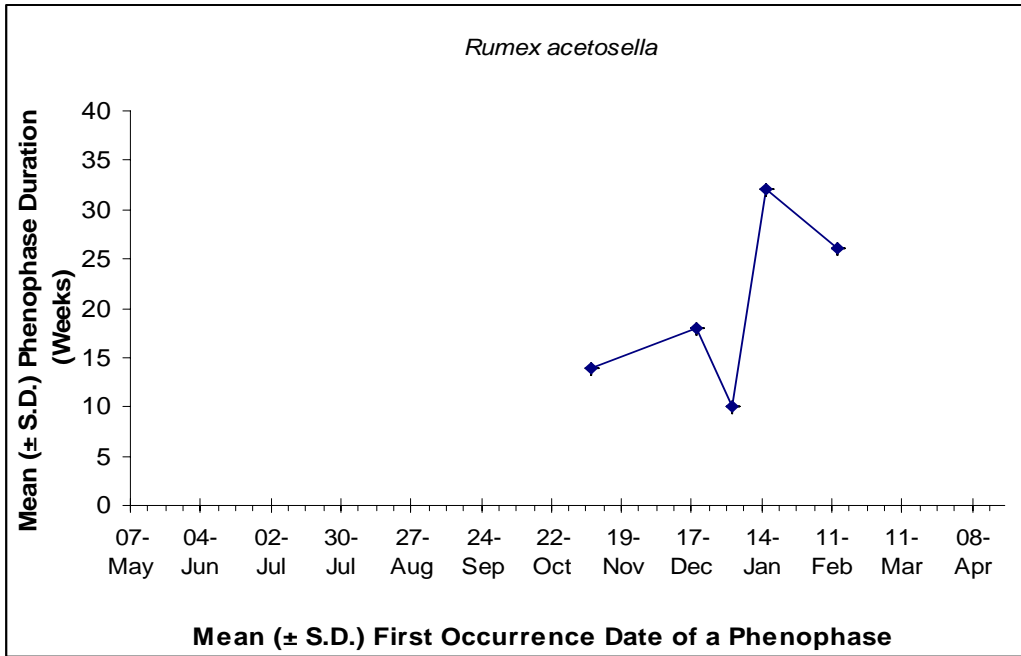


Fig. 2 (K & L): Developmental phenology of K) *P. antiscorbutica* and, L) *R. bitermatus*. Each dot represents mean phenophase timing and duration in sequential order of occurrence from flower buds, flowering, pollen release, fruiting to seed dispersal. The error bars indicate the standard deviation.

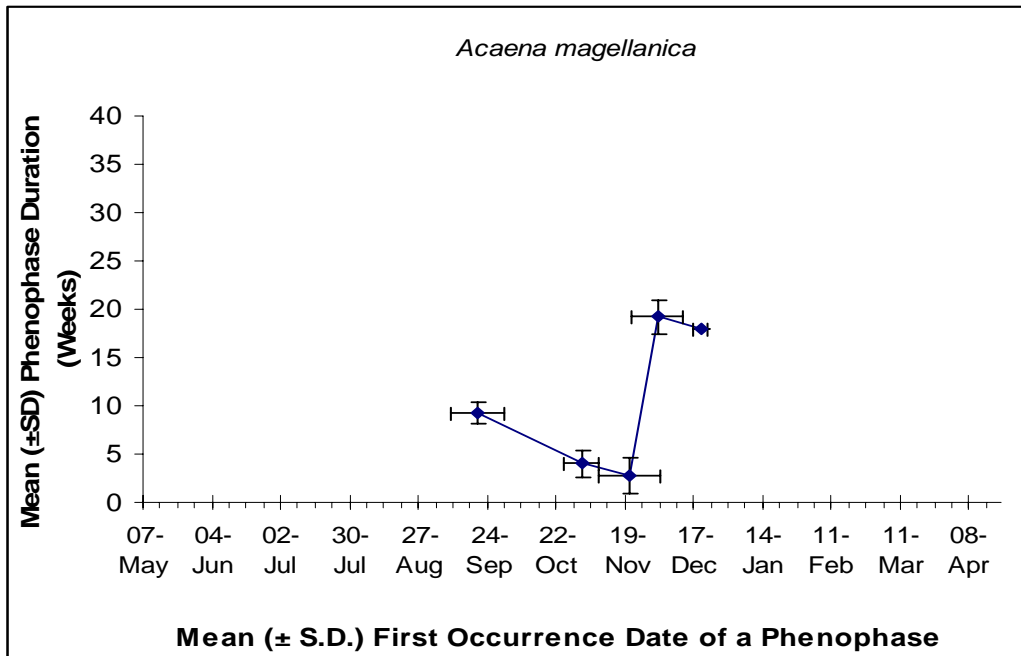
**Herb**

M)



**Shrub**

N)

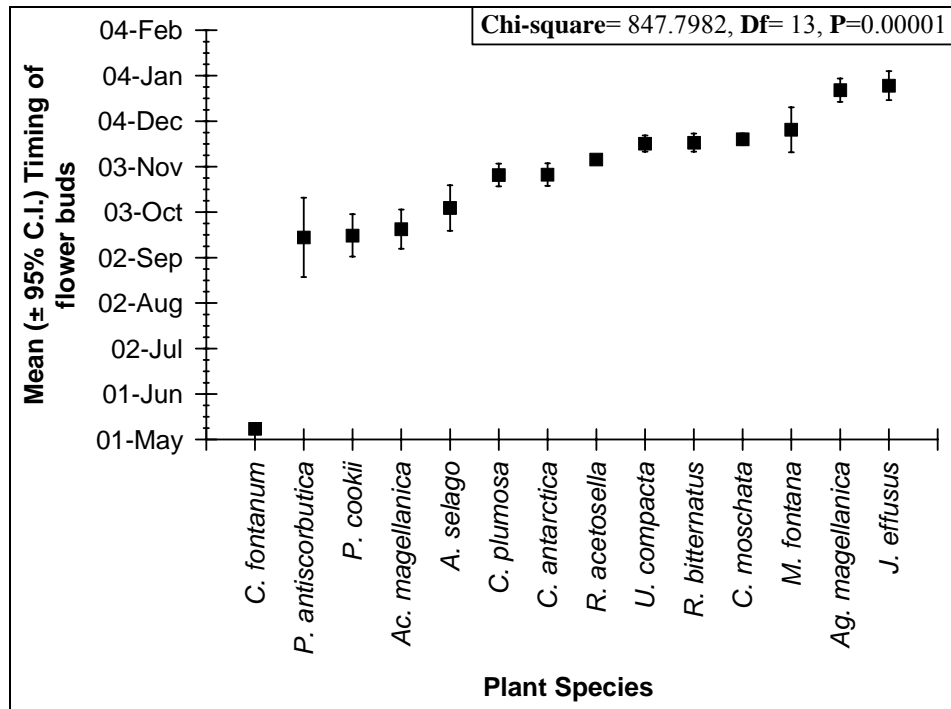


**Fig. 2 (M & N):** Developmental phenology of M) *R. acetosella* and, N) *Ac. magellanica*. Each dot represents mean phenophase timing and duration in sequential order of occurrence from flower buds, flowering, pollen release, fruiting to seed dispersal. The error bars indicate the standard deviation.

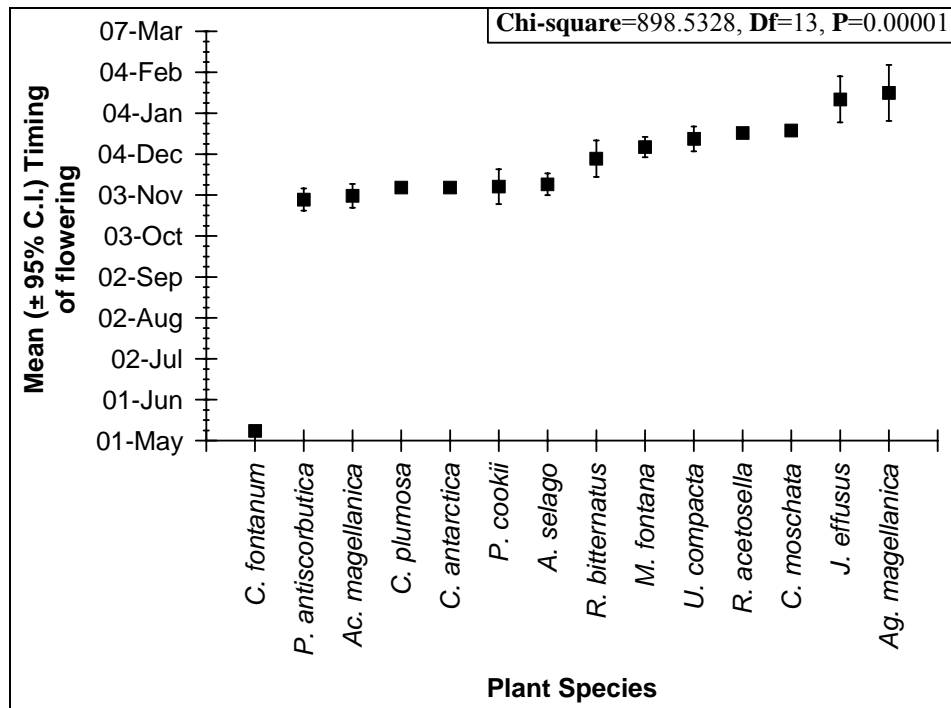
**Table 4:** Mean peak occurrence dates of a phenophase and its standard deviation. Dates were converted from Julian day values into normal calendar dates and standard deviation corresponds to the Julian days around the mean.

<b>Species</b>	<b>Peak flower buds date</b>	<b>± S.D.</b>	<b>Peak flowering date</b>	<b>± S.D.</b>	<b>Peak fruiting date</b>	<b>± S.D.</b>	<b>Peak seed dispersal date</b>	<b>± S.D.</b>
<i>Ag. magellanica</i>	05 Feb	24.2	16 Feb	18.5	11 Mar	6.9	-	-
<i>P. cookii</i>	26 Oct	11.0	01 Dec	14.3	24 Dec	6.7	-	-
<i>Ac. magellanica</i>	23 Oct	9.6	19 Nov	13.2	23 Dec	12.1	26 Dec	7.4
<i>A. selago</i>	05 Nov	6.0	30 Nov	12.2	12 Dec	12.9	-	-
<i>C. antarctica</i>	06 Nov	19.5	12 Dec	9.4	01 Jan	6.2	23 Feb	27.5
<i>C. plumosa</i>	14 Nov	21.1	06 Dec	1.9	09 Jan	13.9	20 Jan	7.3
<i>C. moschata</i>	11 Jan	18.8	16 Jan	2.4	23 Jan	14.4	11 Apr	2.4
<i>M. fontana</i>	10 Jan	51.2	21 Jan	27.6	20 Jan	11.7	28 Jan	11.2
<i>P. antiscorbutica</i>	13 Oct	31.7	22 Nov	18.7	11 Jan	16.4	11 Mar	11.5
<i>R. biternatus</i>	15 Dec	9.5	19 Dec	7.3	08 Jan	11.5	17 Feb	22.0
<i>U. compacta</i>	05 Dec	2.1	26 Dec	6.0	19 Jan	13.9	13 Feb	2.1
<i>C. fontanum</i>	29 Dec	34.7	04 Jan	23.8	22 Jan	23.4	13 Feb	9.0
<i>J. effusus</i>	15 Feb	18.0	15 Jun	28.3	-	-	-	-
<i>R. acetosella</i>	06 Dec	0.0	04 Jan	0.0	17 Jan	0.0	28 Feb	0.0

A)



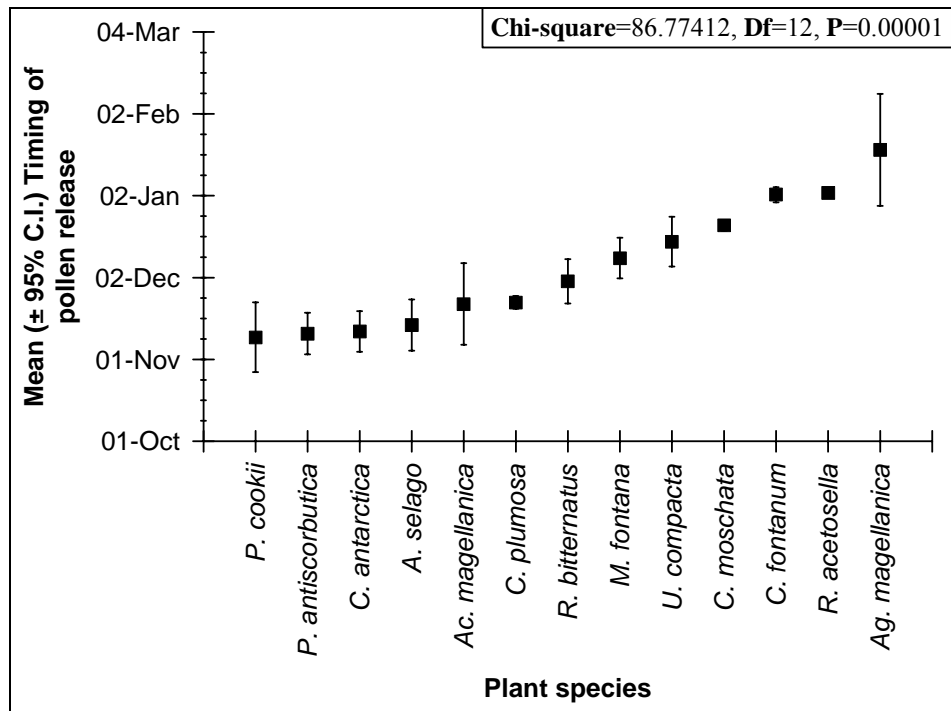
B)



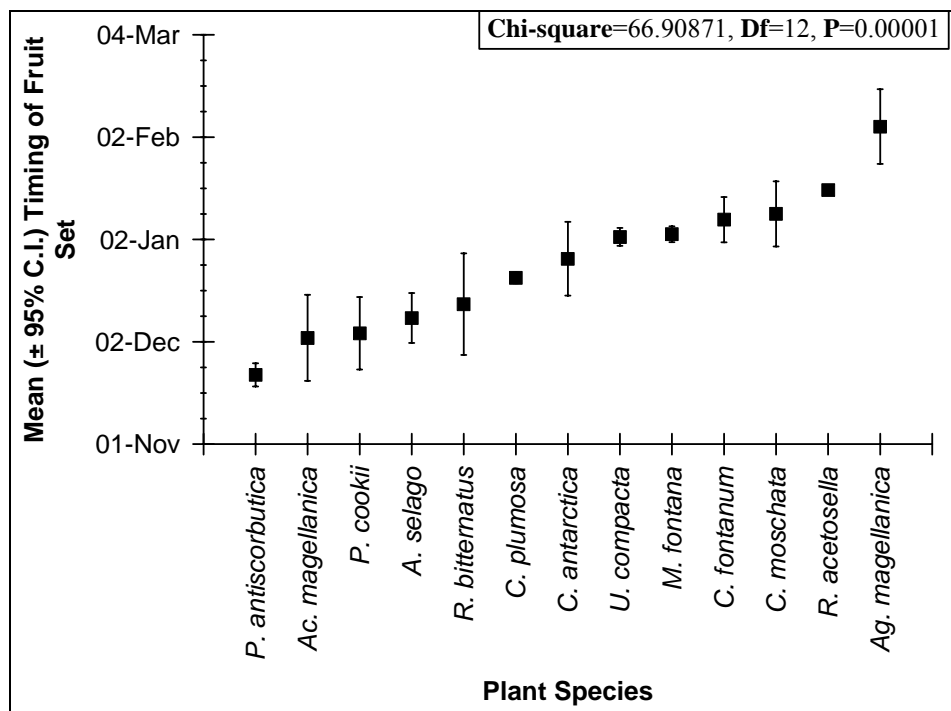
**Fig. 3 (A & B):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes examining species variation in the timing of A) Flower buds and B) Flowering.



C)

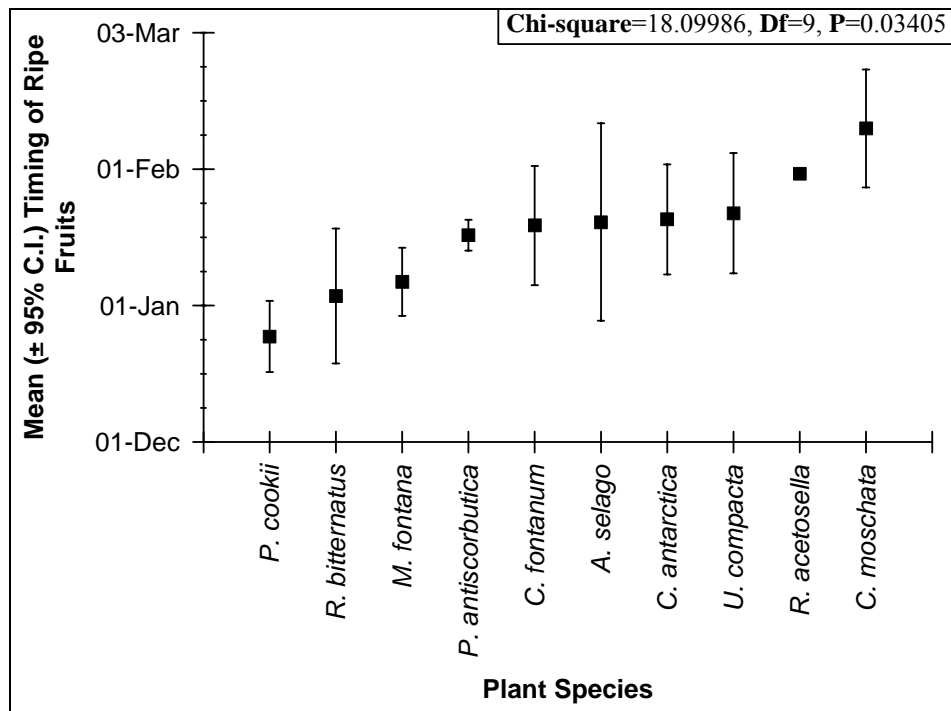


D)

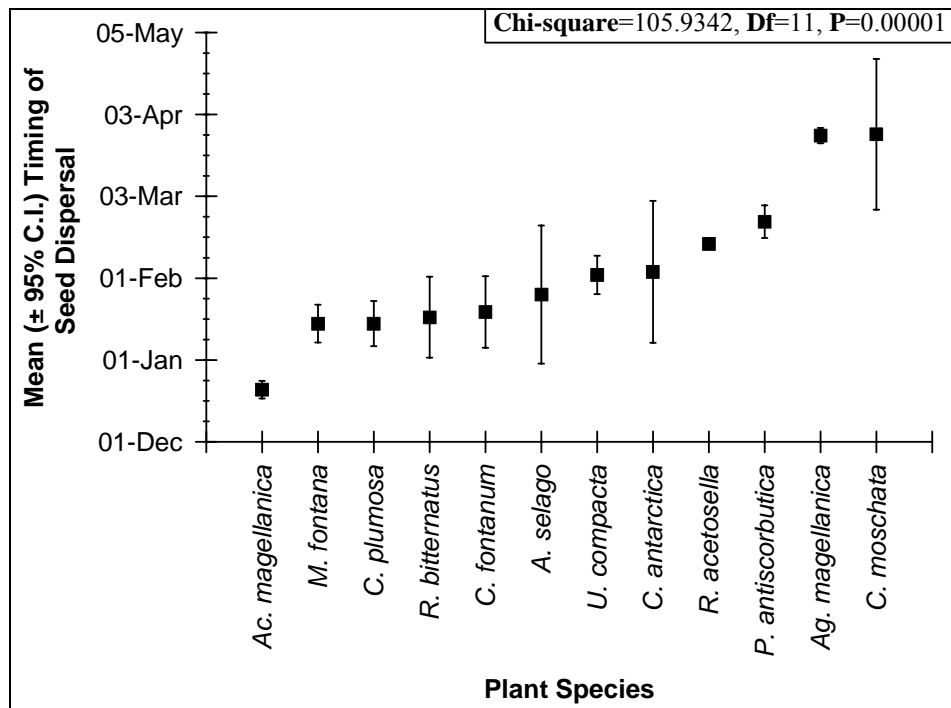


**Fig. 3 (C & D):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes examining species variation in the timing of C) Pollen release and D) Fruit set.

E)

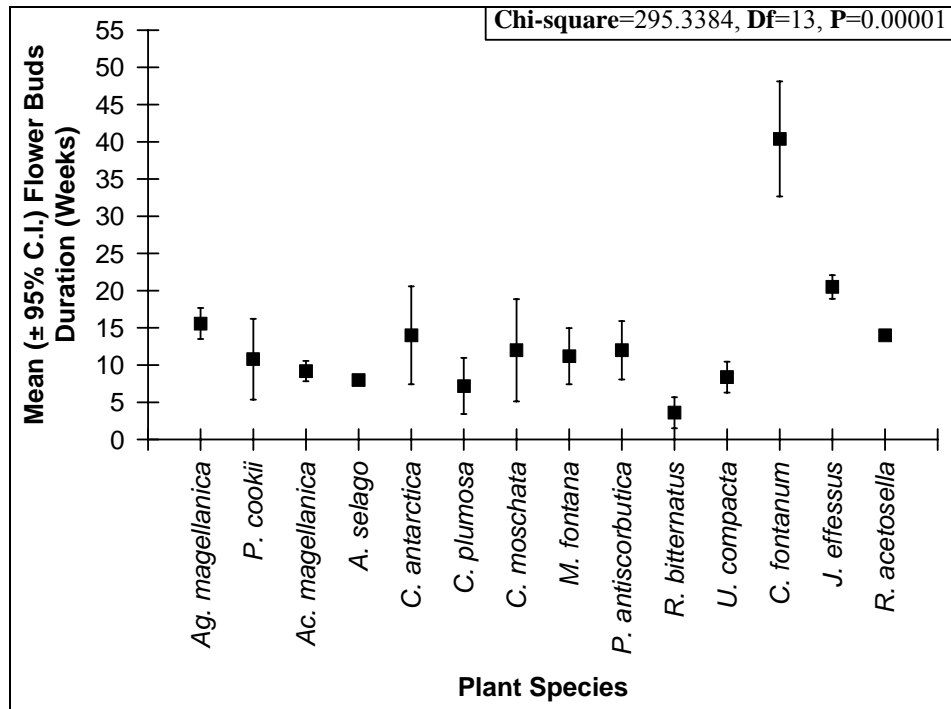


F)

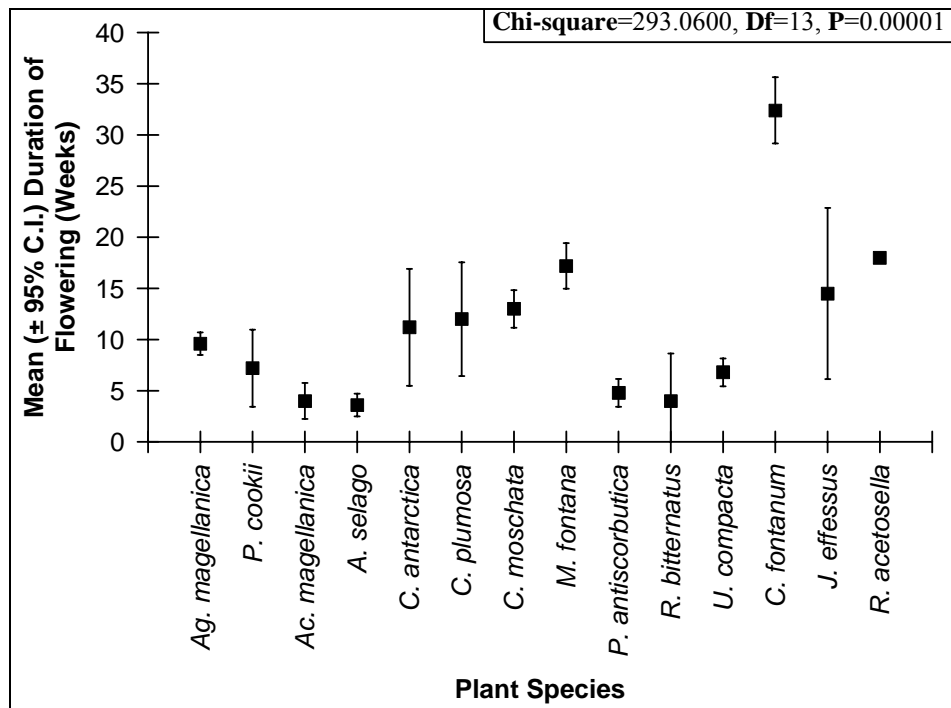


**Fig. 3 (E & F):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes examining species variation in the timing of E) Ripe fruits and F) Seed dispersal.

A)

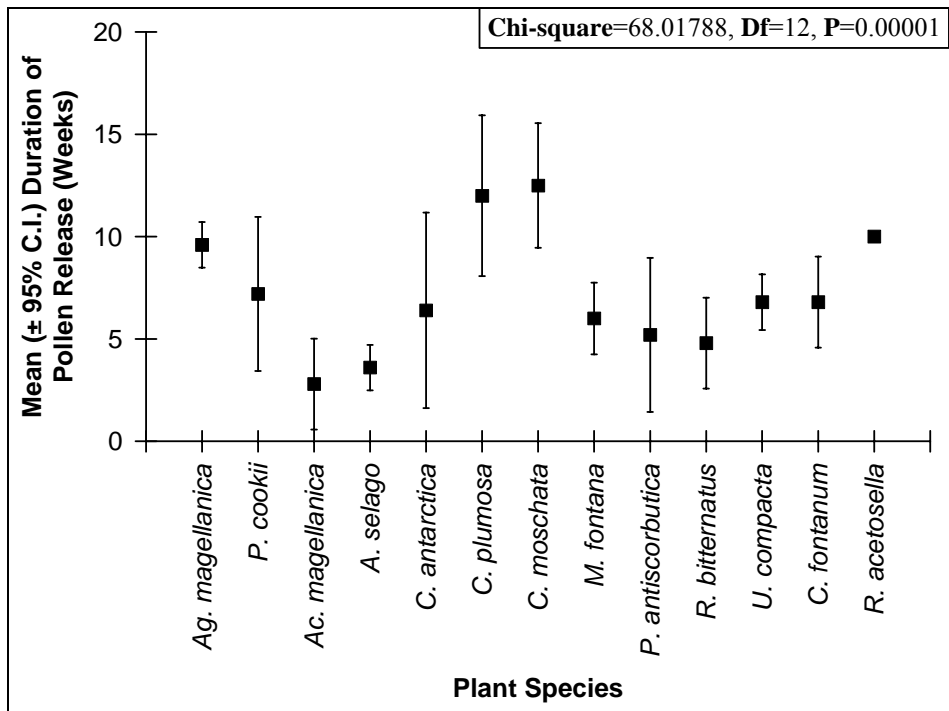


B)

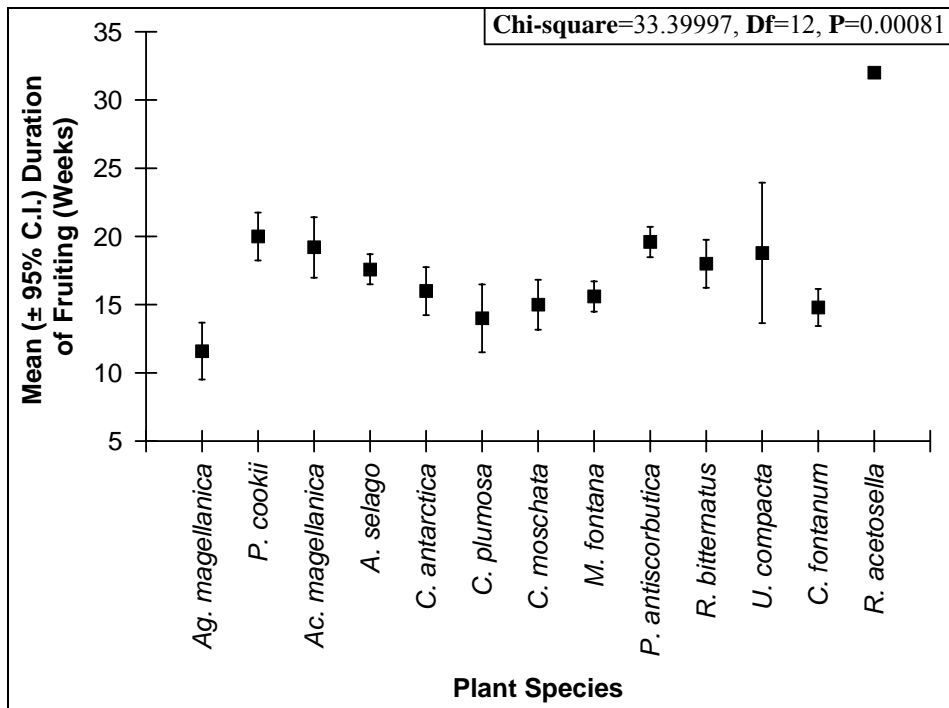


**Fig. 4 (A & B):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes showing the difference between the species A) Flower buds and B) Flowering durations.

C)

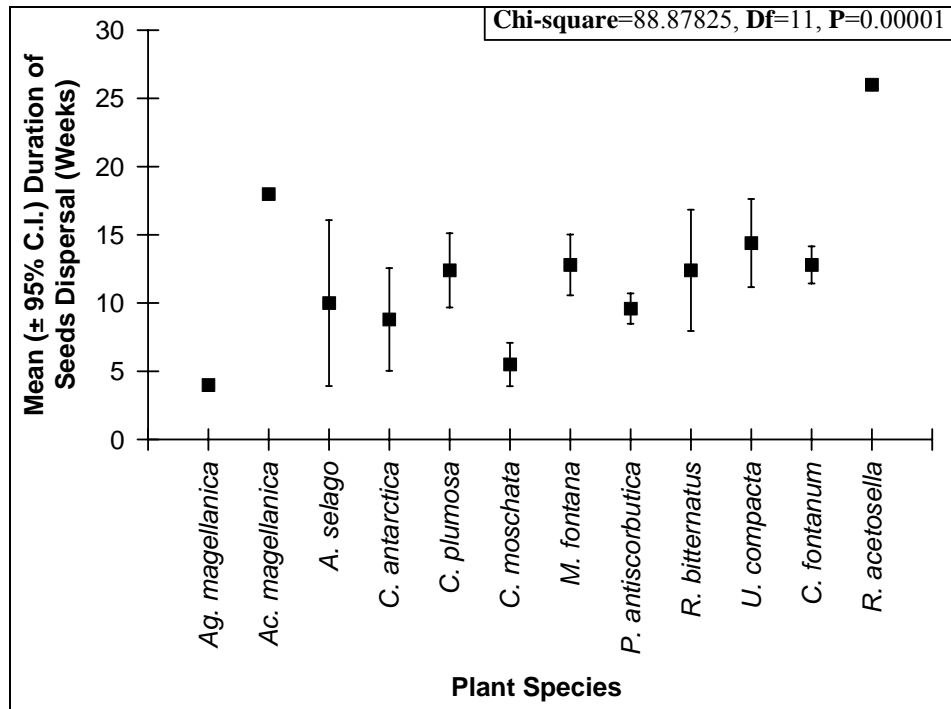


D)



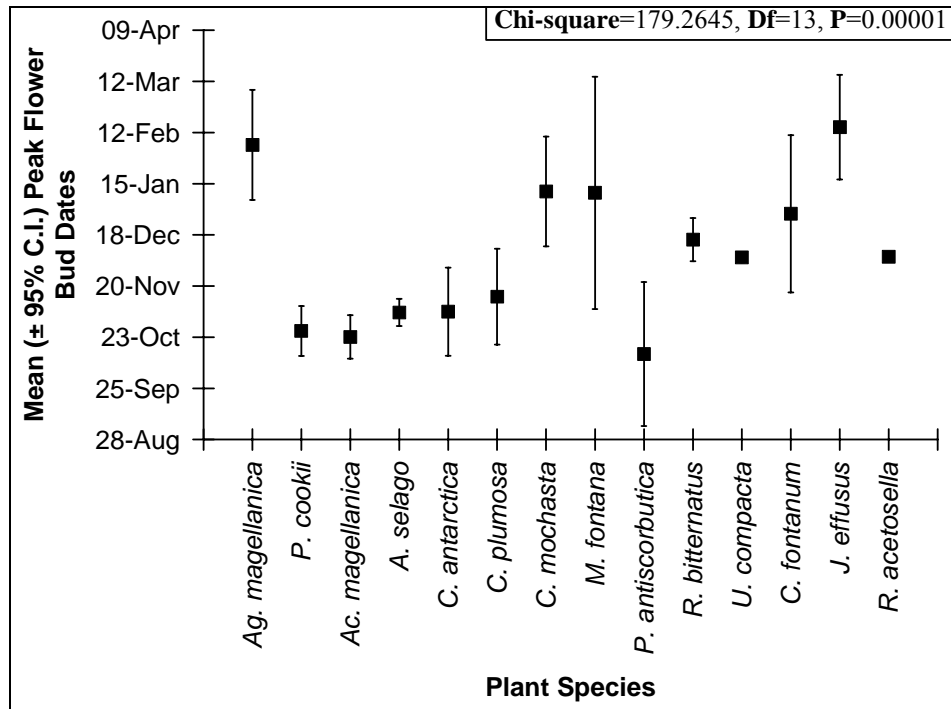
**Fig. 4 (C & D):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes showing the difference between the species C) Pollen release and D) Fruiting durations.

E)

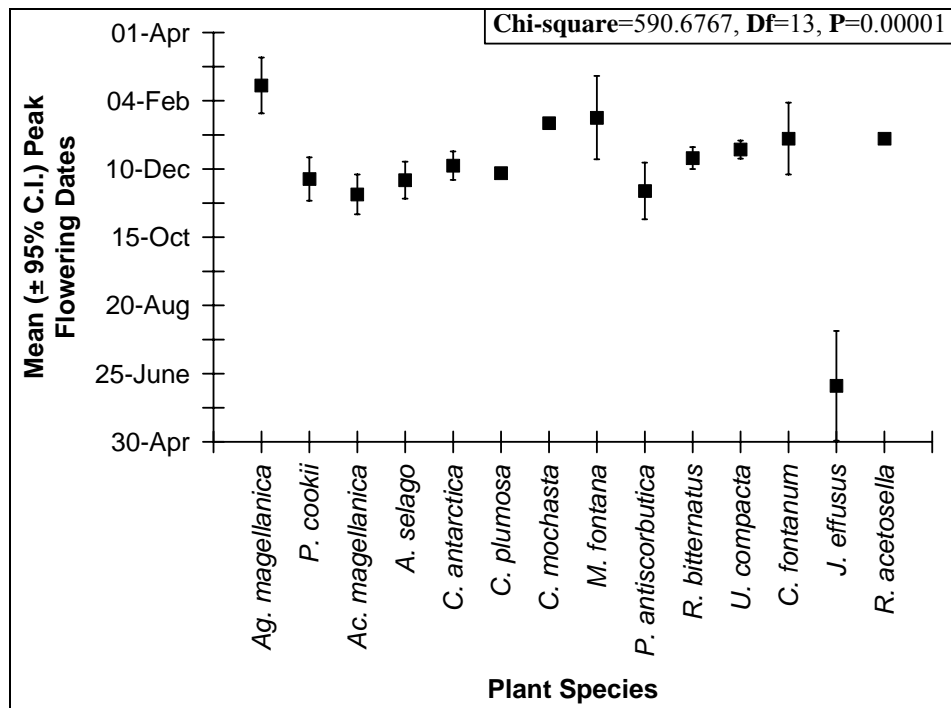


**Fig. 4 (E):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes showing the difference between the species E) Seed dispersal durations.

A)

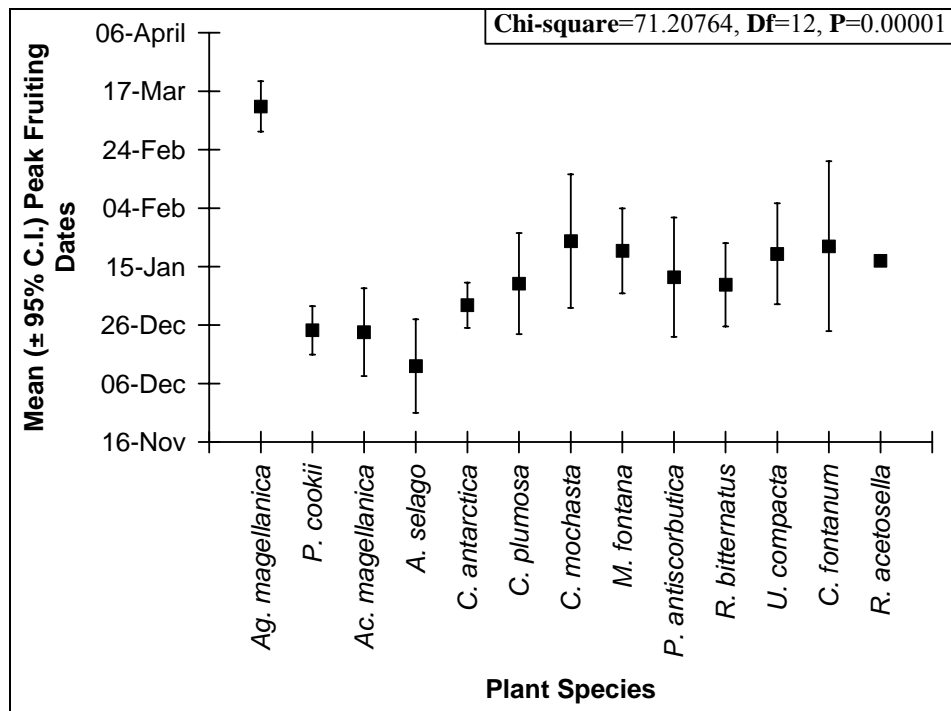


B)

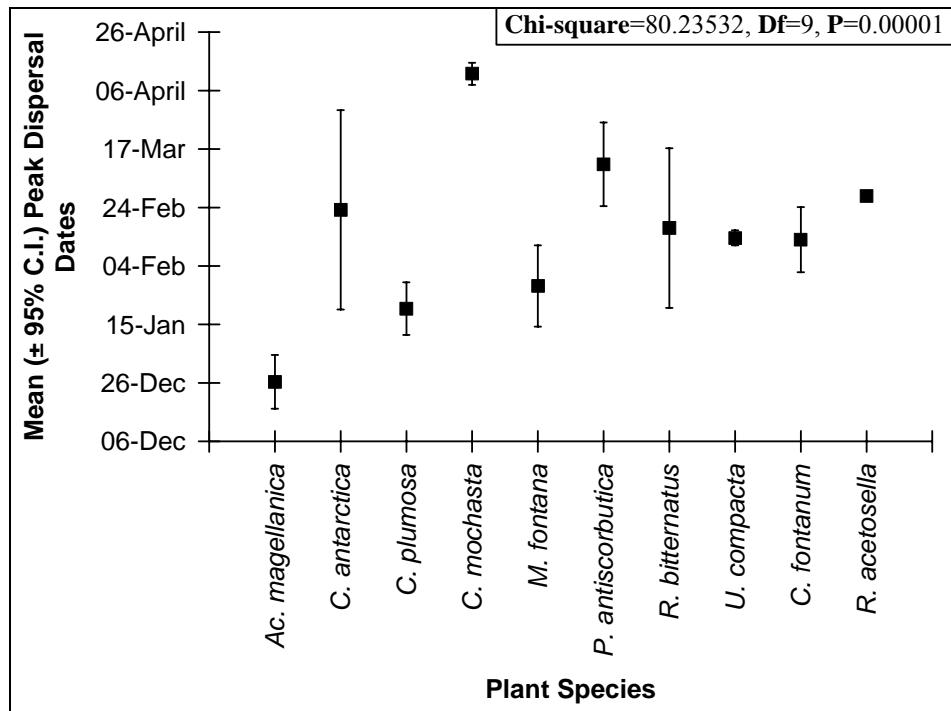


**Fig. 5 (A & B):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes examining the inter-specific differences in peak occurrence dates of A) Flower buds and B) Flowers.

C)



D)



**Fig. 5 (C & D):** Plot of the mean and 95% confidence intervals from the GLZ (Poisson distribution, log-link function, corrected for overdispersion where necessary) outcomes examining the inter-specific differences in peak occurrence dates of C) Fruiting and D) Seed dispersal.

## DISCUSSION

### *Vegetative phenology*

A full year of observation has indicated that vegetative growth occurs throughout the year in most species on Marion Island (**Figs. 1 & 6**). Leaves form, emerge, expand and senesce all year round except in the case of the deciduous shrub *Ac. magellanica* and the cushion plant *A. selago*, which showed winter dormancy. This is not surprising because these findings are consistent with the patterns observed by Smith (1987, 1988) during an investigation of primary productivity of particular habitats (rather than species phenology) on the same island. He indicated that vascular plants on Marion Island have a 10 month growing season. The year-round vegetation growth observed in this study also coincided with patterns displayed by similar species (*C. plumosa*, *C. moschata*, *P. antiscorbutica* and *R. biternatus*) on sub-Antarctic Kerguelen Island (Dorne, 1977; Aubert *et al.*, 1999). The two species that showed winter dormancy on Marion Island, *Azorella selago* and *Acaena magellanica*, also slowed down or halted their growth during winter months on South Georgia and Kerguelen Islands (Dorne, 1977; Walton, 1977a). Contrary to observations on Marion Island *Poa cookii* halted its growth in winter on Kerguelen Island (Dorne, 1977). This is despite the fact that this grass is known as a highly productive species with the ability to photosynthesize throughout the year (Bate & Smith, 1983; Vidal *et al.*, 2003; Gremmen & Smith, 2008). In related Tundra and Alpine communities, heavy winter snowfalls arrest growth by affecting the photosynthetic membrane and CO<sub>2</sub> diffusion activity of plants (Murray & Miller, 1982; Molau, 1993; Starr & Oberbauer, 2003; Marchand *et al.*, 2004; Wipf & Rixen, 2010). Therefore, the absence of permanent snowfalls and high reliance of sub-Antarctic plant growth (photosynthetic activities) on light over temperature (Bate & Smith, 1983; Hennion & Bouchereau, 1998; Aubert *et al.*, 1999), might be contributing to continuous plant growth observed in this study. For instance, the biomass production for *Pringlea antiscorbutica* between 5-12 °C temperature exposures differed little (Hennion & Bouchereau, 1998). Although growth occurs throughout year on Marion Island, elsewhere growth usually takes place during or prior to flowering (Cleland *et al.*, 2006). It was only in *Ac. magellanica* and *A. selago* where plant re-growth in August was immediately followed by reproduction in September.

### *Seasonality of reproductive phenophases*

Data from the current study indicate that Marion Island vascular plants have a pronounced reproductive seasonality. Most species reproductive activities were highly concentrated between the



spring (September) and summer (February) months (**Figs 2 & 6**). This coincided with patterns described in other sub-Antarctic islands such as Kerguelen, Macquarie and South Georgia (Werth, 1911; Taylor, 1955; Tallowin, 1971; Walton, 1977b, 1982; Frenot & Gloaguen, 1994; Bergstrom *et al.*, 1997). For example, all the native and alien plant species on South Georgia Island, including some species examined here, started and concluded their reproductive activities between spring (September) and summer (March) months (Walton, 1982). On Macquarie Island, reproduction of 10 vascular plant species also occurred between November and March (Bergstrom *et al.*, 1997). Therefore, the concentrations of reproductive activities in spring and summer months on temperate sub-Antarctic islands including Marion Island suggest that there is a strong environmental force restricting developmental activities primarily to this period.

In most temperate climates, reproductive phenology is primarily cued by temperature (Rathcke & Lacey, 1985; Wielgolaski, 2003) particularly the mean air temperature of months (one or two) prior to reproduction (Fitter *et al.*, 1995; Sparks *et al.*, 2000; Fitter & Fitter, 2002). Given the small seasonal variation in temperature coupled with unpredictable temperature events on Marion Island (le Roux, 2008), and the fact that reproductive activity started on the same month (September) in which the mean air temperature started to increase slightly (**Fig. 7**; also see le Roux, 2008), the reproductive seasonality observed here cannot be ascribed primarily and exclusively to temperature. Coincidentally, all the plant species examined here initiated their reproductive phenology after appreciable increases in daylength (**Fig. 8**), except for *C. fontanum* which was seen with flowers even in autumn although its peak reproduction by far occurred in spring and summer months. Therefore, relative to temperature, photoperiod may be held accountable for seasonality of reproductive activities observed on Marion Island. The findings that reproductive phenology on Marion Island is regulated by daylength is not a novel one for the sub-Antarctic region, since other studies have demonstrated this before on selected species (Huntley, 1970; Walton, 1977b). However, since no single cue regulates plant phenology individually, small seasonal variation in temperature on Marion Island might be facilitating the role of daylength in driving reproductive phenology (Rathcke & Lacey, 1985; Putterill *et al.*, 2004; Molau *et al.*, 2005; Hänninen *et al.*, 2007). Moreover, the timing mismatches might also eventually occur and drive evolutionary change in the species as temperatures continue to rise with global climate change (Smith, 2002; le Roux & McGeoch, 2008b), but daylength retains its seasonal progression. Indeed, such timing and temperature mismatches are thought to be a primary driver of evolutionary change in other groups (Bradshaw & Holzapfel, 2006, 2010).

### ***Phenological variation***

Although most species showed similar seasonal patterns generally, they individually exhibited a wide range of phenological strategies. Variability was detected in the timing, duration and peak occurrence dates of flower buds, flowering, pollen release, fruiting and seed dispersal. In a given community it is common for species to have varying phenology depending on their respective optimum resource requirements, resource acquisition and allocation capabilities (Castro-Diez *et al.*, 2003; Golluscio *et al.*, 2005; Iversen *et al.*, 2009). On Marion Island, it is possible that the observed phenological variation might be the function of species' idiosyncratic responses to daylength (Corbesier *et al.*, 1996; Purohit & Ranjan, 2002). The species that initiated their reproductive activities earlier in spring (September) respond faster to daylength; while those that set floral buds by late October require intermediate increasing daylength. The late phenology species in the form of *Ag. magellanica* and *J. effusus*, seem to require the longest daylength in summer than the rest of the focal species.

The similarity in onset dates (month) of flower buds and/or flowering events in the sub-Antarctic region co-occurring species further confirm that the timing of developmental activities on these species has evolved to rely largely on photoperiod (see Dorne, 1977; Walton, 1982; Bergstrom *et al.*, 1997; Aubert *et al.*, 1999; Broughton & McAdam, 2005). For example, *Ac. magellanica* (Falklands and South Georgia), *M. fontana* (Falklands, Macquarie and South Georgia), *C. antarctica* (South Georgia), *P. antiscorbutica* (Kerguelen), *R. biternatus* (Falklands, Kerguelen and South Georgia), *A. selago* (Falklands and Kerguelen), *C. plumosa* (Kerguelen), *C. moschata* (Kerguelen), *P. cookii* (Kerguelen) and *Ag. magellanica* (Falklands) individually started their relative floral activities during the same month as on Marion Island. Furthermore, the timing of flower buds or flowers on *Poa cookii* on Marion Island is similar to *Poa flabellata* on the Falkland Islands and on South Georgia (Walton, 1982; Broughton & McAdam, 2005). While *Uncinia compacta* floral timing on Marion Island coincided with that of *Uncinia meridensis* on South Georgia (Walton, 1982). On the contrary, some species including the ones mentioned as budding or flowering at the same month in more than one island, have been observed with flower buds or flowers approximately one to two months later or earlier than on Marion Island (see Dorne, 1977; Walton, 1982; Bergstrom *et al.*, 1997; Broughton & McAdam, 2005), although this was not common.

As is the case on Marion Island the first occurrence date of flowering coincided with pollen release activity or at least occurred within short interval on most species documented on South Georgia (Walton, 1982). Despite the fact that most sub-Antarctic plant species have more or less similar flower bud set or flowering dates, their respective timing of fruit ripening varied substantially (Dorne, 1977; Walton, 1982; Bergstrom *et al.*, 1997) indicating that other external factors jointly with photoperiod influence fruit ripening dates, but this hypothesis was not tested in this study. On Kerguelen Island the fruit ripening dates on *Pringlea antiscorbutica* coincided with longer photoperiod and relatively higher temperatures in summer (Aubert *et al.*, 1999). Although the homogenous species grouping (early, middle and late phenology species) was only evident during flower bud set, flowering and dispersal phenophases; it is clear that Marion Island temperate system is no different to other systems comprised of many plant species (Molau, 1992; Thórhallsdóttir, 1998; Kudo & Suzuki, 2002; Molau, *et al.*, 2005). One conflicting factor in this comparison is the latitudinal variation in daylength of the summer solstice and the rate of daylength change (**Fig. 9**). Thus both variables increase with latitude, which might confound assessments of the relative contribute of temperature and daylength to differences in plant phenology on the islands.

Besides the fact that different species may require varying optimum resources to initiate and maintain their life-history (species idiosyncratic response), there is also a possibility that the observed phenological variation (timing, peak and duration) might have resulted from other ecological processes or controlled by species phylogenetic constraints (Wright & Calderon, 1995; Bolmgren & Cowan, 2008) which were not tested in this study. Coincidentally, on Marion Island, *P. antiscorbutica* and *A. selago* required the longest time for their seeds to mature, and to compensate for this time they were amongst the earliest species to set flower buds (see Bolmgren & Cowan, 2008). Similarly, on Macquarie Island, Bergstrom *et al.* (1997) grouped species phenology as rapid, slow and very slow depending on the time a species required to complete its developmental activities. Like on Marion Island, *M. fontana*, was the fastest species to complete its life-cycle.

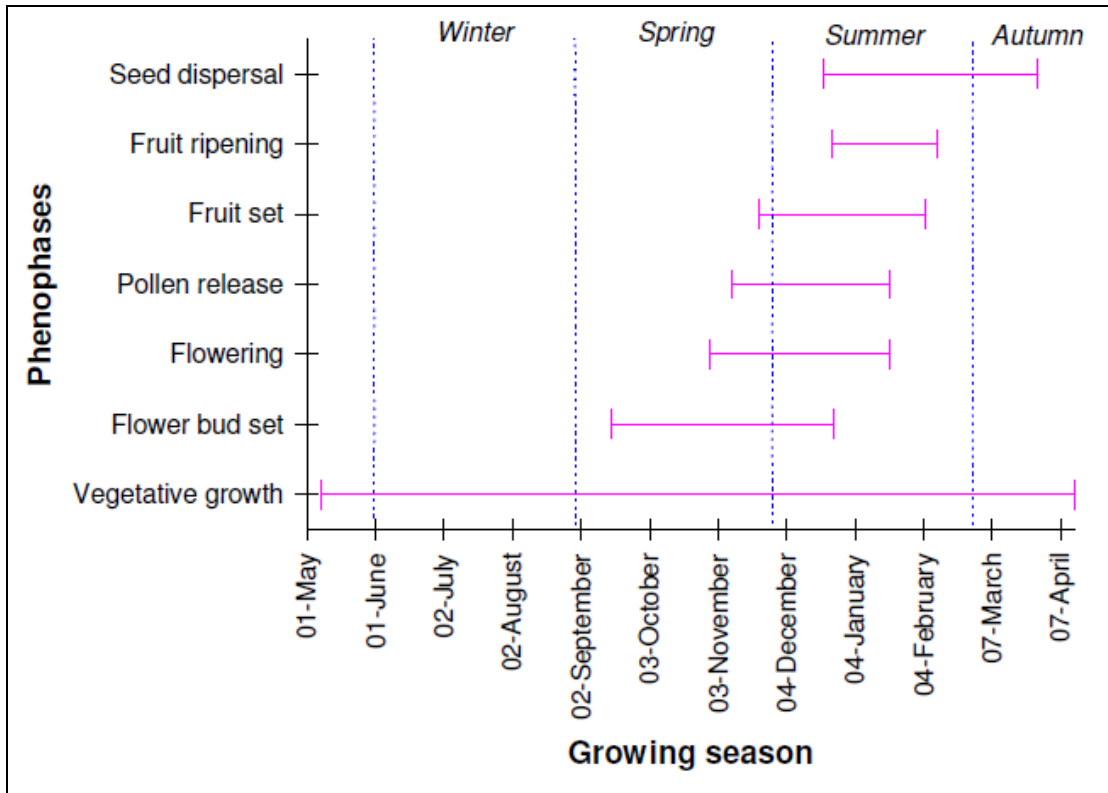
### ***Aliens versus indigenous plant species***

Different from the rest of indigenous and other two alien plant species, an alien *C. fontanum* was observed flowering in autumn before the start of 2007 spring/summer although it reached its reproduction peak during spring and summer months on Marion Island. The autumn flowering displayed by this species is probably not explained by daylength. However, its peak reproduction

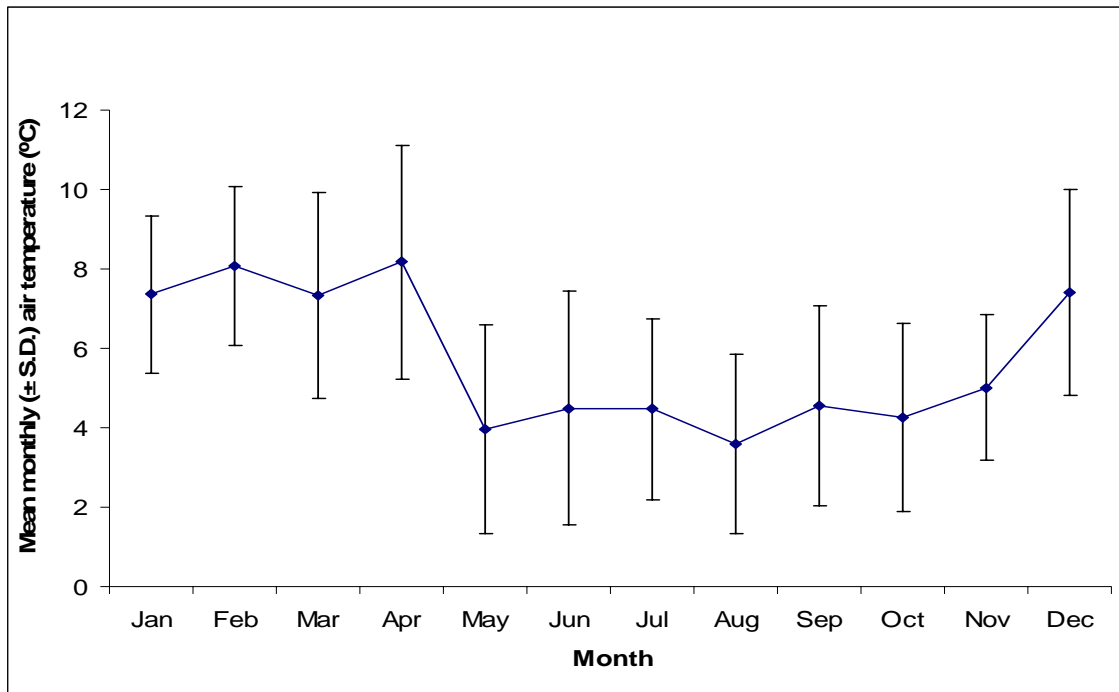
dates occurred months later in summer when daylength is relatively longer and therefore daylength might act as a cue for early season flowering (**Fig. 8**). In its native range, Southern Sweden, *C. fontanum* is strictly a summer flowering plant (Bergfur *et al.*, 2004). However, on Marion Island this species was found flowering for most part of the year. This is not surprising because many successful invaders have high phenological plasticity and in an invaded range, they often flower earlier or later and for longer than natives to gain a competitive reproductive advantage (Meyer, 1998; Zotz *et al.*, 2000; Daehler, 2003; Godoy *et al.*, 2009). On most sub-Antarctic islands including Marion Island, *C. fontanum* has a versatile reproductive biology and this trait might be contributing largely to its success in the region (Gremmen, 1975; Ramaswiela *et al.*, in preparation). Other alien plant species, *R. acetosella* and *J. effusus* had similar phenology to the rest of the plant species on Marion Island. Coincidentally, these species are the only alien plant species still restricted to their probable points of introduction.

## **CONCLUSION**

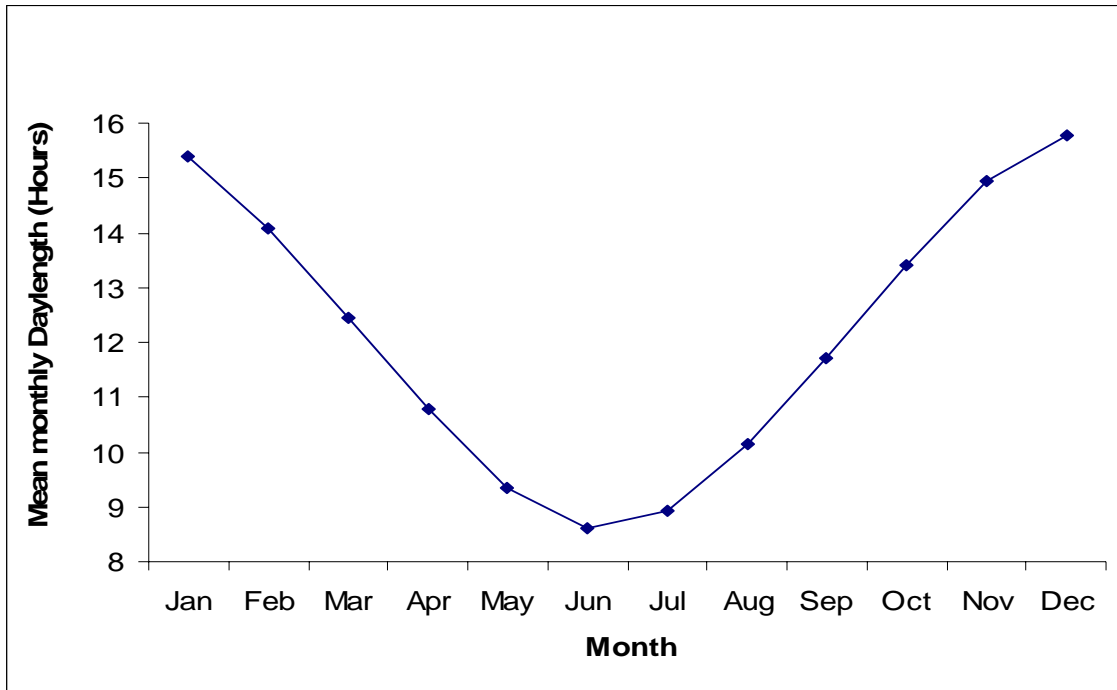
The current study has indicated that plants grow throughout the year but reproductive activities primarily occur during spring/summer months on sub-Antarctic Marion Island. *Cerastium fontanum* was the only species that reproduced for most of the year, and this may be one reason for its rapid spread as an invasive species (Ramaswiela *et al.*, ms. in preparation). However, the other two alien species investigated here had reproductive phenology following similar seasonal patterns to the indigenous plant species. Although most species show seasonality there is a great variation in the phenophase timing, duration and peak occurrence date between species suggesting varying, species-specific patterns.



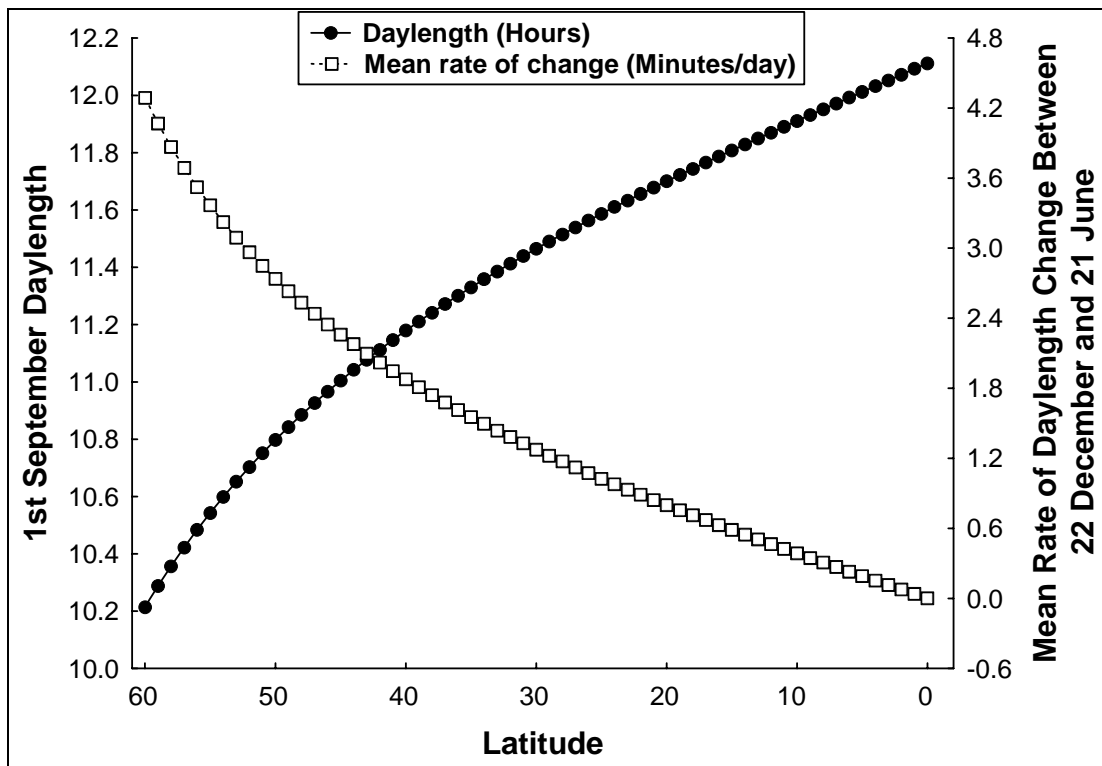
**Fig. 6:** The range of mean first occurrence dates of all phenophases across spring and summer flowering species surveyed on Marion Island. Dotted lines indicate austral seasons.



**Fig. 7:** Seasonal variation in air temperature on Marion Island (Year 2007). Error bars indicate standard deviation.



**Fig. 8:** Annual variation in daylength on sub-Antarctic Marion Island. Standard deviation bars were omitted for clarity.



**Fig. 9:** Daylength variation and rate of change across latitudes. Error bars on the right Y-axis were omitted for clarity.

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## INTRODUCTION

Many plant species have evolved to rely on seasonal variation in climate to time their reproductive activities to coincide with favourable periods (Rathcke & Lacey, 1985). Based on this climate-plant relationship, for centuries plant phenology was primarily used to predict the local weather conditions (Schwartz *et al.*, 1997; Sparks & Menzel, 2002). Much more recently, the growing concern for documenting, monitoring and predicting the impact of climate change on biodiversity has further increased the scope and interest of phenology (Miller-Rushing *et al.*, 2007). In consequence, phenology, particularly that of plants, has become one of the most reliable bioindicators of climate change (Spano *et al.*, 1999; Sparks & Menzel, 2002; Parmesan & Yohe, 2003). Warmer than typical springs in recent years have been linked with earlier flowering in a wide range of plant species (Fitter *et al.*, 1995; Menzel *et al.*, 2006a; Bertin, 2008; Miller-Rushing *et al.*, 2008). At the same time, flowering phenology of some plant species has remained relatively unchanged, while for others is occurring later than is typical of the species concerned (Abu-Asab *et al.*, 2001; Fitter & Fitter, 2002; Menzel *et al.*, 2006b). Similarly, different reproductive phenophases of an individual species are also showing a contrasting response to environmental change (Post *et al.*, 2008; Hoffman *et al.*, 2010). Indeed, climate change is having considerable impacts on seasonal behaviour of plant species globally (Rosenzweig *et al.*, 2008 and references therein). If a shift in phenology of each plant species or a phenophase of an individual species is symmetrical to that of interacting species, there would not be any impact on plant fitness. Regrettably, rates of phenological response to climate change vary substantially with trophic levels (Sherry *et al.*, 2007; Doi *et al.*, 2008; Willis *et al.*, 2008) and this may lead to loss of relative timing between naturally interacting species in a given community (Harrington *et al.*, 1999; Both *et al.*, 2009). These alterations will not only have dire ramifications for the species-level, but will also affect ecosystem structure and functioning as whole (Doi *et al.*, 2008; Willis *et al.*, 2008).

Because of these potential implications, it is of fundamental importance to monitor species seasonal behaviour in response to climate change. Unfortunately, investigations of phenological responses to recent environmental change are concentrated in Northern Hemisphere systems owing to the presence of long-term reference data often spanning centuries (see data listing in Rosenzweig *et al.*, 2008). The paucity of long-term phenological records in the Southern Hemisphere has largely limited the usage of phenology in climate change research (Wolfe *et al.*, 2005; Thuiller, 2007;

Rosenzweig *et al.*, 2008), although a few studies have demonstrated phenological changes (see Jarrad *et al.*, 2008; Petrie & Sadras, 2008; Gallagher *et al.*, 2009). Typical of many Southern Hemisphere systems, little has been done in the sub-Antarctic region to monitor the seasonal variability of plants in response to documented environmental change despite the importance of the region for addressing significant scientific questions, particularly the ways in which climate change may differentially affect Southern and Northern systems (Bergstrom & Chown, 1999; Chown *et al.*, 2004; le Roux & McGeoch, 2008a). Nevertheless, lack of historical and recurring phenology records to use as a basis of investigation on sub-Antarctic region doesn't necessarily equate to lack of species response to current environmental change (see Thompson & Clark, 2006; Clark & Thompson, 2009).

Documented temperature increases in the sub-Antarctic region (Frenot *et al.*, 1997; Bergstrom & Chown, 1999) might have had pronounced effects on phenology, since temperature is typically limiting (Rathcke & Lacey, 1985; Parmesan & Yohe, 2003; Root *et al.*, 2003). Lately, changes in the distribution and abundance of selected vascular plant species on sub-Antarctic Marion Island have been linked with warmer temperature and declining precipitation (Chown & Smith, 1993; le Roux & McGeoch, 2008a). Furthermore, experimental study has demonstrated the sensitivity of a keystone species, *Azorella selago*, to changes in temperature and precipitation patterns on the same island (le Roux *et al.*, 2005). However, to date, the synergistic impact of precipitation changes and warming on phenological dynamics has not been monitored on this island, despite the presence of once-off phenological investigations of the majority of vascular plant species undertaken in the 1965/66 (hereafter referred to as 1965) growing season (Huntley, 1970). Although the study was observed over one growing season, it remains the only information that can be used in highlighting the direction of any phenological shifts on the island (see Hülber *et al.*, 2010). Furthermore, the outcome may also be suggestive of the future responses of flora on the sub-Antarctic Marion Island and elsewhere in the region. Therefore, this study was undertaken primarily to monitor the impact of climate change on the timing of selected reproductive phenophases.

## **MATERIALS AND METHODS**

### **Study Site**

This study was conducted on the eastern side of sub-Antarctic Marion Island (46°54' S, 37°45' E). Marion Island is a young volcanic landmass of approximately 290 km<sup>2</sup> in size, located in the vast

southern Indian Ocean (McDougall *et al.*, 2001; Chown & Froneman, 2008; Lutjeharms & Anson, 2008). Typical of oceanic islands, Marion Island experiences a thermally stable hyper-oceanic climate (wet, cool and windy) which over the years has undergone considerable changes (Smith & Steenkamp 1990; le Roux, 2008). The mean annual temperature increased from 5.3°C in the 1960s to 6.5°C in the 2000s, with the greatest warming having occurred in late summer months relative to other seasons (Smith, 2002; le Roux & McGeoch, 2008b). The mean annual precipitation, which mostly comes in a form of rain at low-altitude sites, is currently 1975 mm, a decline from approximately 3000 mm in the 1960s (le Roux & McGeoch, 2008b). Along with these changes in climate considerable biological changes were also recorded on the same island (Smith & Steenkamp, 1990; Chown & Smith, 1993; le Roux & McGeoch, 2008b) and if current rate of climate change continues further impacts are expected (le Roux *et al.*, 2005; McGeoch *et al.*, 2006).

### **Study Species**

The historical study by Huntley (1970) recorded the absolute first occurrence dates of three phenophases (flowering, pollen release and fruit ripening) of 12 indigenous vascular plant species in lowland populations namely: *Acaena magellanica*, *Agrostis magellanica*, *Azorella selago*, *Blechnum penna-marina*, *Callitriche antarctica*, *Cotula plumosa*, *Crassula moschata*, *Juncus scheuchzerioides*, *Montia fontana*, *Pringlea antiscorbutica*, *Poa cookii* and *Uncinia compacta*. This study included ten of these species (i.e. *Blechnum penna-marina* and *Juncus scheuchzerioides* were excluded – see below). Here I review briefly the biology and distribution of these species, focusing on information from Marion Island.

### ***Acaena magellanica* Lam. Vahl. (Rosaceae)**

This species may survive in wet, dry or mesic habitats. However, it achieves its optimum growth on Drainage Line slopes (Walton, 1982; Gremmen *et al.*, 1998). Self-compatible inflorescences are produced early in the season after substantial increase in daylength (Huntley, 1970; Walton, 1977, 1982). At anthesis it takes approximately two months for inflorescences to develop into matured fruits (Walton, 1982; Hennion & Walton, 1997). In recent years, the altitudinal distribution of this species was found to have expanded upslope by approximately 22 m and this has coincided with the warmer and drier climate on Marion Island (le Roux & McGeoch, 2008a).

***Agrostis magellanica* Lam. (Poaceae)**

On Marion Island *Ag. magellanica* is dominant on low-altitude sites with high moisture level, although it has an altitudinal limit of 743 m (le Roux & McGeoch, 2008a). This grass species may be found growing as epiphyte on *Azorella selago* cushions (Gremmen & Smith, 2008). The flowering of this hygrophilous species commences between November and December after the sizeable increase in daylength (Huntley, 1970).

***Azorella selago* Hook. f. (Apiaceae)**

*Azorella selago* is a long-lived and slow-growing cushion plant occurring from the coastline to 840 m a.s.l. on Marion Island (Huntley, 1970; le Roux & McGeoch, 2008a). Although *A. selago* is widespread and ubiquitous on Marion Island, it dominates the Fellfield vegetation communities (Gremmen & Smith, 2008). As a keystone species, this cushion plant is regarded as the most important plant species on the island (Barendse & Chown, 2001; Hugo *et al.*, 2004; le Roux & McGeoch, 2004; le Roux *et al.*, 2005). Flowering phenology of this species is more responsive to photoperiod than any other cue, thus setting flowers by mid-September (Huntley, 1970). An experimental study undertaken on Marion Island has indicated that warming and drying may lead to the advancement of autumnal senescence (le Roux *et al.*, 2005). This in turn might affect other species that depend on this species for resources and/or shelter (Hugo *et al.*, 2004).

***Callitriche antarctica* Engelm. ex Hegelm. (Callitrichaceae)**

As a nitrophile, *C. antarctica* is predominately found on biotically nitrogen-enriched coastal mud habitats with high moisture levels and often forms hanging carpets on seal wallows (Whinam, 1989; Vidal *et al.*, 2003). The altitudinal limit of this plant species remained relatively constant at 535 m despite warmer and drier climate experienced over four decades on the island (le Roux & McGeoch, 2008a). Flowers set by late September (Huntley, 1970) exhibit a geitonamous pollination system through anemophily (Philbrick & Anderson, 1992; Philbrick & Les, 2000; Ackerman, 2000) or hypohydrophily (Philbrick, 1993).

***Cotula plumosa* Hook. f. (Asteraceae)**

This mat-forming, halophilous plant species grows in lowland coastal habitats characterised by biotic activities and recurrent exposure to salt-spray (Huntley, 1970, 1971; Turner *et al.*, 2006; Gremmen & Smith, 2008). Against the general patterns of species movement to cooler higher altitudes in response to warming, this species contracted its altitudinal distribution range by 16 m to

49 m a.s.l. (le Roux & McGeoch, 2008a). Despite the species ability also to reproduce vegetatively (Turner *et al.*, 2006), its floral phenology is cued by both photoperiod and temperature (Huntley, 1970).

***Crassula moschata* Forst. f. (Crassulaceae)**

*Crassula moschata* is also a halophilous plant species occurring mostly on rocky coastal salt-sites, and typically it is tolerant to frequent salt deposition (Huntley, 1971). Similar to its co-occurring species, *C. plumosa*, *Crassula moschata* also contracted its range down-slope (le Roux & McGeoch, 2008a). Substantial increase in photoperiod and temperature during September is thought to drive the commencement of flowering activities of this plant on Marion Island (Huntley, 1970).

***Montia fontana* L. (Portulacaceae)**

*Montia fontana* is common on coastal areas which are biotically influenced but it may grow in other habitats quite a distance from the coast, up to 607 m a.s.l (Huntley, 1970; Gremmen & Smith, 2008; le Roux & McGeoch, 2008a). Depending on habitat conditions this fast growing plant species may self-pollinate and/or display self-compatibility to produce dark brown to black seeds (Walton, 1982; Bergstrom *et al.*, 1997).

***Poa cookii* Hook. f. (Poaceae)**

This is a highly productive grass species common and dominant in biotically influenced habitats along the coast and close to sea-bird nests inland up to 659 m in altitude (Bate & Smith, 1983; Gremmen & Smith, 2008; le Roux & McGeoch, 2008a). Although, this grass can grow on less nutrient-rich habitats it rarely reaches its optimum growth. At low-altitude sites, *P. cookii* flowers in late August in response to daylength (Huntley, 1971).

***Pringlea antiscorbutica* R. Br. (Brassicaceae)**

The ability of this species to withstand various harsh climatic conditions enables it to survive and reproduce on variety of vegetation communities from very low to high altitude (Hennion & Walton, 1997; Hennion & Bouchereau, 1998). The altitudinal range of this species expanded from 260 to 494 m a.s.l. within four decades on Marion Island (Huntley, 1970; le Roux & McGeoch, 2008a). Amongst the focal species, *P. antiscorbutica*'s range expansion to cooler higher altitude sites was by far the greatest (le Roux & McGeoch, 2008a). The reproductive phenology of this Kerguelen

cabbage, which commences in September, coincides with an increase in temperature and daylength on Marion Island (Huntley, 1970).

### ***Uncinia compacta* R. Br. (Cyperaceae)**

*Uncinia compacta* is a moisture- and temperature-sensitive sedge which is well distributed on dry mires below 400 m a.s.l on Marion Island (Huntley, 1970; Chown & Smith, 1993; le Roux & McGeoch, 2008a). The drying and warming associated with climate change on Prince Edward Islands seem to be increasing the dominance of this sedge on mires (Chown & Smith, 1993). A previous study has showed that this sedge flowers approximately by early January (Huntley, 1970).

### **Sampling Design**

Huntley's survey was conducted fortnightly and opportunistically without any permanent sites in 1965 growing season (Huntley, 1970). In essence, Huntley recorded the absolute timing of three phenophases (flowering, pollen release and fruit ripening) fortnightly across low-populations areas on Marion Island (eastern side of the island). However, phenological data was also collected opportunistically outside the prescribed fortnight schedule, perhaps daily. To examine the phenological responses of these plants to warming and declining precipitation, a second phenological study was undertaken in the 2007/2008 growing season (hereafter referred to as 2007), except that in the current survey observations were made in a more systematic fashion: fortnightly on five, 5 m x 5 m permanent plots per species except for *C. moschata* where only four sites were used (see Chapter 2 for comprehensive methods). The second study aimed also to quantify in a more systematic fashion the variation in phenology within species, but had the drawback that it complicated comparison with the older data (**Table 1**; see also Miller-Rushing *et al.*, 2008). Observations were not conducted on *Juncus scheuchzerioides* and *B. penna-marina* and on *Ac. magellanica*, *Ag. magellanica* and *C. plumosa* the fruit ripening date could not be determined in the 2007 survey due to their complexity. Given that the observed phenophases were not clearly defined in the historical study, there might have been differences in the way in which phenophases were defined in the two studies particularly flowering and fruit ripening phenophases.

### **DATA ANALYSIS**

The absolute earliest timing of each of the phenophases for each of the species was recorded in the 2007 season and converted to Julian days. Those recorded by Huntley in 1965 were likewise converted to Julian days. To determine the number of days in which an event has shifted to either

direction, the difference between the current and historical phenophase timing (in Julian days) was calculated i.e. 2007-1965 record. Depending on whether the current phenophase record was earlier, later or remained unchanged the resultant values were either negative, positive or zero, respectively. Because sampling was fortnightly in the 2007 study and daily in 1965 (assumed from Huntley's (1970) description of the methods used), the maximum difference in phenophase that can be attributed to sampling frequency differences is 13 full days (**Table 1**). Therefore, phenophase responses were also adjusted by 13 days (always in the direction of a delay in 2007 relative to 1965 because of the direction of the sampling frequency asymmetry) to determine what the maximum effect of sampling differences is likely to have been. The 2007 absolute earliest and mean first occurrence date of phenophase records were also tabled to determine the differences between the absolute earliest dates of an event and the mean timing thereof. Furthermore, the 95% confidence intervals of the mean timing of phenophases from the 2007 data were used to see if the 1965 values lie within these confidence intervals.

## RESULTS

Summary data for the phenophases of the species, in Julian days, are provided for the 2007 survey (**Table 2**) and for the 1965 survey (**Table 3**) for comparative purposes. **Table 4** provides a comparison for these two sets of phenological data based on the absolute difference in the date and its significance determined from 95% confidence intervals of the mean date presented in **Table 2**. The absolute first occurrence date of reproductive phenophases differed between 2007 and 1965 growing season (**Table 4**), with the trend towards later phenological development. Eighty percent of the investigated vascular plant species flowered substantially later in 2007 than in 1965. The timing of pollen release was more variable among species. Species either delayed, advanced or remained relatively unchanged in their pollen release date (**Table 4**). Similar to flowering phenophase, the majority of species delayed their fruit ripening dates in 2007 by comparison with 1965, except in the case of *U. compacta* where ripe fruit were observed earlier (**Table 4**). On average, the absolute timing of flowering, pollen release and fruit ripening was delayed by 33.2, 5.4 and 13.8 days, respectively (**Table 4**). To make the assessment of the phenological studies as comparable as possible, the maximum sampling frequency discrepancies was accounted for (see **Table 4**). This procedure reduced the substantial timing differences in absolute phenophase and in mean phenophase, and in some instances a species phenophase changed the phenological direction (**Table 4**). On average, and having corrected for maximum sampling differences, the pollen release date advanced by 2.0 days in 2007 compared with 1965. However, the absolute timing of flowering and

fruit ripening on average remained delayed by 23.0 and 4.5 days, respectively (**Table 4**). Although there was variation in absolute phenophase timing between 2007 and 1965, the 1965 timing values of flowering on *Ag. magellanica* and *C. plumosa*; pollen release on *A. selago*, *C. antarctica* and *C. plumosa*, and fruit ripening on *M. fontana* lie within the modified 95% confidence intervals of 2007 mean first occurrence date (**Table 2 & 4**). That is to say, there were no significant differences between the 2007 and 1965 values of the aforementioned phenophases for the respective species. However, the timing of the entire phenophases of *Uncinia compacta* occurred significantly earlier in 2007 than in 1965 (i.e. 1965 values are larger than the 2007 95% confidence intervals). Similarly, *Ag. magellanica* and *P. antiscorbutica* also significantly advanced their pollen release date in 2007 relative to 1965. Except for these species and/or specific phenophases, the reproductive events occurred significantly later in 2007 overall (**Table 4**).

## DISCUSSION

Although many studies have recorded distinct responses of plant species and/or individual species phenophases to warming (Fitter & Fitter, 2002; Post *et al.*, 2008; Miller-Rushing & Inouye, 2009), the most common trend at the regional and global scales is a shift towards earlier timing (see Parmesan & Yohe, 2003; Studer *et al.*, 2005; Rosenzweig *et al.*, 2008). Despite the shifts being variable among plant assemblages the trend is often in the same direction (see **Table 5**). On average, the timing of events for species in Britain, for example, has advanced by 4.5 days (Fitter & Fitter, 2002). Contrary to these trends, the majority of the plant species investigated here significantly delayed their phenology in 2007 relative to 1965 despite recorded temperature increases (Smith, 2002; le Roux & McGeoch, 2008b). On average, indigenous species delayed their flowering, pollen release and fruit ripening time by 33.2, 5.4 and 13.8 days, respectively. Correcting for sampling frequency reduced the average number of days in which species phenophases were delayed, but it did little to change the phenological direction of species except on pollen release. Although it's rare for community assemblages to retard their phenology as substantial as in this study, similar patterns have been observed elsewhere (Taylor & Garbary, 2003; Chambers & Keatley, 2010). For example, plants species in Canada significantly delayed their flowering time by 45 days, on average despite warmer climate (Taylor & Garbary, 2003). Similarly, the species pollen release, and fruit ripening ranges on Marion Island are within the flowering deviation extremes (-55 to +36) recorded by Fitter & Fitter (2002) for warmer seasonal temperate system. Thus, although the responses documented here might at first appear unusual, they do fit within the scope of the variation seen globally, especially if corrected for possible sampling bias (noting that this is a



maximum correction). Nonetheless, several site-specific factors might also help to explain the trend found on Marion Island.

Most significantly, in the sub-Antarctic region, perhaps due to its aseasonality (Chown *et al.*, 1998; Bergstrom & Chown, 1999; le Roux, 2008) temperature appears to be less important relative to seasonal progression of photoperiod in regulating reproductive phenology (Huntley, 1970; Walton, 1977; Aubert *et al.*, 1999). This is further confirmed by the fact that in the sub-Antarctic region, co-occurring plant species and/or shared genera tend to flower or set floral buds during the same month despite varying mean annual temperature across these islands (see Chapter 2; Chown *et al.*, 1998). Even in warmer than typical springs the sensitivity of plant to daylength as a primary cue for reproductive phenology ensures that floral development only commences when optimum daylength requirements (shorter or longer) have been met or exceeded (Corbesier *et al.*, 1996; Keller & Körner, 2003; Thuiller, 2007). Given the steady state of seasonal photoperiod progression, the substantial phenological changes detected here are unexpected from photoperiod sensitive plant species despite warming (Keller & Körner, 2003; Thuiller, 2007; Rosenzweig *et al.*, 2008). It is therefore plausible that the later phenological development exhibited by Marion Island photoperiod sensitive plant species might have been a function of other causal factors apart from climate change. Recording discrepancies from the reference study by Huntley (1970) may be especially significant. For instance, the pollen release date for *Acaena magellanica* is reported as earlier in Huntley (1970) than in Huntley (1971), and *C. moschata* flowered later in Huntley's (1968) thesis relative to Huntley (1970) despite the data having been collected by a single observer, at the same time and on the same island. Interestingly, the timing of open flowers on *Acaena magellanica* in Huntley (1970) is earlier than that of floral buds in Huntley (1971). I quote "*In common with Azorella selago, Poa cookii and Pringlea antiscorbutica, the phenological behaviour of Acaena adscendens is daylength stimulated. Young foliar buds appear in July, despite the fact that snow falls with increasing frequency until late September when mean temperatures starts to rise again. The buds are protected by large scales until ready to burst into leaf in late August. By October a dense canopy of leaves covers the moss carpet, floral buds appear, and pollination commences early in December.*" - Huntley, 1971 (pp. 134). For comparison purpose, see **Table 3** reproduced from the Huntley (1970) paper.

Indeed, these recording discrepancies are problematic and thus, it is not entirely clear if the reproductive phenology of indigenous plant species on Marion Island has changed with changing

climate. If indeed the observed phenological delay is real and verified later, it may be expected that these changes could have been caused by the now drier climate (le Roux, 2008) or the synergism of drier and warmer climate (Jentsch *et al.*, 2009; van Dijk, 2009). Furthermore, such an overall delayed phenology pattern would not be novel as other work has demonstrated this elsewhere (Taylor & Garbary, 2003; Chambers & Keatley, 2010).

## **CONCLUSION**

The findings of this study should be taken with caution. Firstly, there seem to be recording discrepancies in the Huntley (1970) reference data and this makes it difficult to determine phenological change. Therefore, either the Marion Island plant species really have mostly delayed their overall reproductive phenology following their thermal peculiarities or the observed shifts are a function of recording discrepancies. Secondly, only two years of data sets were analysed while it is recommended that at least 20 years of recurring data be analysed to accurately detect biological changes (see review by Tooke & Battey, 2010). However, because of the scarcity of long-term phenological records on Marion Island these findings are ideal for highlighting the direction of any phenological shift. Furthermore, the current results provide a baseline data upon which future phenological change associated with climate change could be determined.

**Table 1:** Sampling frequency differences between the historical and current studies. Zero is the day in which observation started in all studies (current and historical). NS (i.e. No Sampling) indicates the days in which observations were not made in the current study while 1 denotes opportunistic sampling days in the historical study.

Sampler/Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Huntley 1970	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2007 study	0	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	1
Maximum difference	13														

**Table 2:** The absolute, mean and 95% confidence intervals (C.I.) of first occurrence date (Julian days) of reproductive phenophases of indigenous vascular plant species on Marion Island for the 2007 growing season. Empty cells indicate the phenophases which were not observed in the 2007/08 growing season. Numbers in parentheses indicate the modified C.I. values i.e. Original value minus 13 days.

Species	Flowering				Pollen Release				Fruit Ripening			
	Absolute	Mean	-95% C.I.	+95% C.I.	Absolute	Mean	-95% C.I.	+95% C.I.	Absolute	Mean	-95% C.I.	+95% C.I.
<i>P. cookii</i>	298	313	300 (287)	327 (314)	298	313	300 (287)	327 (314)	353	359	351 (338)	367 (354)
<i>Ac. magellanica</i>	297	306	297(284)	315 (302)	311	326	311 (298)	341 (328)				
<i>A. selago</i>	311	315	307 (294)	323 (310)	311	318	308 (295)	328 (315)	367	385	363 (350)	407 (394)
<i>C. antarctica</i>	310	313	310 (297)	315 (302)	310	316	308 (295)	323 (310)	371	386	373 (360)	398 (385)
<i>P. antiscorbutica</i>	295	304	295 (282)	312 (299)	309	315	307 (294)	323 (310)	379	382	378 (365)	386 (373)
<i>M. fontana</i>	338	343	336 (323)	351 (338)	338	343	336 (323)	351 (338)	366	371	364 (351)	379 (366)
<i>C. plumosa</i>	310	313	310 (297)	315 (302)	324	327	324 (311)	329 (316)				
<i>C. moschata</i>	354	356	354 (341)	358 (345)	354	356	354 (341)	358 (345)	394	406	393 (380)	420 (407)
<i>Ag. magellanica</i>	367	384	363 (350)	406 (393)	367	384	363 (350)	406 (393)				
<i>U. compacta</i>	340	350	340 (327)	359 (346)	340	350	340 (327)	359 (346)	371	387	373 (360)	401 (388)

**Table 3:** The absolute first occurrence date (Julian days) of reproductive phenophases of indigenous vascular plant species on Marion Island in the 1965 growing season.

<b>Species</b>	<b>Absolute Earliest Date</b>		
	<b>Flowering</b>	<b>Pollen release</b>	<b>Fruit ripening</b>
<i>P. cookii</i>	241	269	325
<i>Ac. magellanica</i>	255	283	339
<i>A. selago</i>	255	311	339
<i>C. antarctica</i>	269	297	339
<i>P. antiscorbutica</i>	269	311	353
<i>M. fontana</i>	269	311	353
<i>C. plumosa</i>	297	311	353
<i>C. moschata</i>	297	325	368
<i>Ag. magellanica</i>	368	395	427
<i>U. compacta</i>	368	395	427

**Table 4:** Changes in the first occurrence date of phenophases (absolute) of indigenous vascular plant species on Marion Island between 1965 and 2007. Values in parentheses indicate the responses of a phenophase after having accounted for possible effects of sampling frequency differences between the studies. Positive values indicate phenophase delay and negative values advance.

<b>Species</b>	<b>Absolute Earliest Date Change in Days</b>		
	<b>Flowering</b>	<b>Pollen release</b>	<b>Fruit ripening</b>
<i>P. cookii</i>	57 (44) <sup>-*</sup>	29 (16) <sup>-*</sup>	28 (15) <sup>-*</sup>
<i>Ac. magellanica</i>	42 (29) <sup>-*</sup>	28 (15) <sup>-*</sup>	
<i>A. selago</i>	56 (43) <sup>-*</sup>	0 (-13) <sup>nc</sup>	28 (15) <sup>-*</sup>
<i>C. antarctica</i>	41 (28) <sup>-*</sup>	13 (0) <sup>nc</sup>	32 (19) <sup>-*</sup>
<i>P. antiscorbutica</i>	26 (13) <sup>-*</sup>	-2 (-11) <sup>+*</sup>	26 (13) <sup>-*</sup>
<i>M. fontana</i>	69 (56) <sup>-*</sup>	27 (14) <sup>-*</sup>	13 (0) <sup>nc</sup>
<i>C. plumosa</i>	13 (0) <sup>nc</sup>	13 (0) <sup>nc</sup>	
<i>C. moschata</i>	57 (44) <sup>-*</sup>	29 (16) <sup>-*</sup>	26 (13) <sup>-*</sup>
<i>Ag. magellanica</i>	-1 (-12) <sup>nc</sup>	-28 (-15) <sup>+*</sup>	
<i>U. compacta</i>	-28 (-15) <sup>+*</sup>	-55 (-42) <sup>+*</sup>	-56 (-43) <sup>+*</sup>
<b>Range</b>			
<i>Uncorrected</i>	-28 to +69	-55 to +29	-56 to +32
<i>Corrected</i>	-15 to +56	-42 to +16	-43 to +19
<b>Mean</b>			
<i>Uncorrected</i>	33.2	5.4	13.8
<i>Corrected</i>	23.0	-2.0	4.5

Note: <sup>-\*</sup> = Significant delay based on 95% confidence intervals from Table 2.

<sup>+\*</sup> = Significant advance based on 95% confidence intervals from Table 2.

NC= No significant change based on 95% confidence intervals from Table 2.

**Table 5:** Observations of plant phenological trends in responses to increasing temperature. Positive values indicate phenophase delay and negative values advance. Empty cells indicate the absence of data. Temperature increases denote the mean annual temperature and in other cases increases of months prior reproduction.

Location	Phenophase	Phenological change (days)		Temp. increase (°C)	References
		Mean	Range		
Europe	Flowering		-20 to +20	0.6	Ahas <i>et al.</i> , 2002
Europe	Flowering	-37.6		1.7	Luterbacher <i>et al.</i> , 2007
Germany	Flowering		-2.6 to -6.9	1	Menzel <i>et al.</i> , 2005
Switzerland	Full-Bloom	-20		1.5	Defila & Clot, 2005
Britain	Flowering	-1.94	-19 to +39		Kirbyshire & Bigg, 2010
Poland	Flowering	-14		2.7	Sparks <i>et al.</i> , 2009
Japan	Flowering	-5.5		1.8	Miller-Rushing <i>et al.</i> , 2007
Korea	First bloom		-0.5 to -2.4	2	Ho <i>et al.</i> , 2006
Concord, Massachusetts, USA	Flowering	-7		2.4	Miller-Rushing & Primack, 2008
North Eastern USA	Flowering		-2 to 12.7		Wolfe <i>et al.</i> , 2005
Washington DC, USA	Flowering	-2.4	-46 to +10	1.2	Abu-Asab <i>et al.</i> , 2001
Australia	Leaf break, leaf fall, flowering, peak flowering, ripe fruits and Harvesting	+0.6	+0.3 to +0.9	0.02	Chambers & Keatley, 2010

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This study is the first to document comprehensively and systematically the vegetative and reproductive phenologies (or aggregate phenological patterns) of twelve indigenous (*Acaena magellanica*, *Agrostis magellanica*, *Azorella selago*, *Blechnum penna-marina*, *Callitriche antarctica*, *Cotula plumosa*, *Crassula moschata*, *Poa cookii*, *Pringlea antiscorbutica*, *Ranunculus biternatus* and *Uncinia compacta*) and three alien (*Cerastium fontanum*, *Juncus effusus* and *Rumex acetosella*) vascular plant species on Marion Island. The differences found among the species and distinct seasonal groupings (e.g. early and late species) were also assessed. I also determined the phenological differences among the indigenous and alien plant species. Furthermore, this study recorded the impact of climate change on the timing of selected phenophases, although this comparison was compromised somewhat by discrepancies in reporting in the earlier studies (Huntley, 1968, 1970, 1971).

This study showed that plant growth occurs throughout the year on Marion Island except in the case of two indigenous species, *A. selago* and *Ac. magellanica*, which halted or slowed down their growth in winter. Previous work at the habitat scale has confirmed the long growing season of vascular plants at the Prince Edward Islands (Smith, 1987, 1988). Similarly, the plant growth patterns observed here are also consistent with the patterns displayed by respective species on sub-Antarctic Kerguelen and South Georgia Islands (Dorne, 1977; Walton, 1977a; Aubert *et al.*, 1999). Certainly, the continuous plant growth exhibited by most plant species investigated here is typical of the region, because sub-Antarctic vascular plant growth predominately relies on light relative to temperature (Bate & Smith, 1983; Hennion & Bouchereau, 1998; Aubert *et al.*, 1999). However, distinct from most vascular plants on sub-Antarctic region the photosynthetic activities of a cushion plant, *A. selago* and deciduous shrub, *Ac. magellanica* appear to be primarily regulated by temperature, rather than any other cues (Dorne, 1977; Walton, 1977a). Contrary to Marion Island, *P. cookii* halted its growth in winter months on Kerguelen Island (Dorne, 1977) despite the fact that this grass is known to photosynthesize throughout the year (Bate & Smith, 1983; Vidal *et al.*, 2003; Gremmen & Smith, 2008).

The reproduction in most species followed a strongly seasonal pattern (between spring and summer months) (**Fig. 1**). It was only in *Ag. magellanica* and *C. moschata* where the last component of reproduction (dispersal) occurred in autumn (March). The seasonality of reproductive activities on



Marion Island is not surprising as other phenological works on Kerguelen, Macquarie, Falklands and South Georgia demonstrated similar patterns, although for Kerguelen Island reproductive season is the broadest (see **Fig. 2**, Taylor, 1955; Werth, 1911; Tallowin, 1971; Walton, 1977b, 1982; Frenot & Gloaguen, 1994; Bergstrom *et al.*, 1997; Broughton & McAdam, 2005). Furthermore, some species and/or clades occurring on Marion Island and other sub-Antarctic islands showed similar flowering onset date (see **Fig 3**; Dorne, 1977; Walton, 1982; Bergstrom *et al.*, 1997; Aubert *et al.*, 1999; Broughton & McAdam, 2005). For example, the flower buds/flowering month of *Ac. magellanica* (Falklands and South Georgia), *M. fontana* (Falklands, Macquarie and South Georgia), *C. antarctica* (South Georgia), *P. antiscorbutica* (Kerguelen), *R. biternatus* (Falklands, Kerguelen and South Georgia), *A. selago* (Falklands and Kerguelen), *C. plumosa* (Kerguelen), *C. moschata* (Kerguelen), *P. cookii* (Kerguelen) and *Ag. magellanica* (Falklands) were similar to that found on Marion Island (**Fig. 3**). Since there are no large changes in temperature between seasons in the region (Bergstrom & Chown, 1999; Smith, 2002; le Roux, 2008) and that photoperiod is the most likely cue that changes with seasons, these patterns suggest that sub-Antarctic species' reproduction have evolved to primarily rely on daylength (Huntley, 1970; Walton, 1977b). However, the overall differences in fruit ripening and dispersal time by the respective species/shared genera across sub-Antarctic islands ( See **Fig. 3**; Dorne, 1977; Walton, 1982; Bergstrom *et al.*, 1997) suggests that other external factors perhaps in association with photoperiod influence the timing of these events (Aubert *et al.*, 1999).

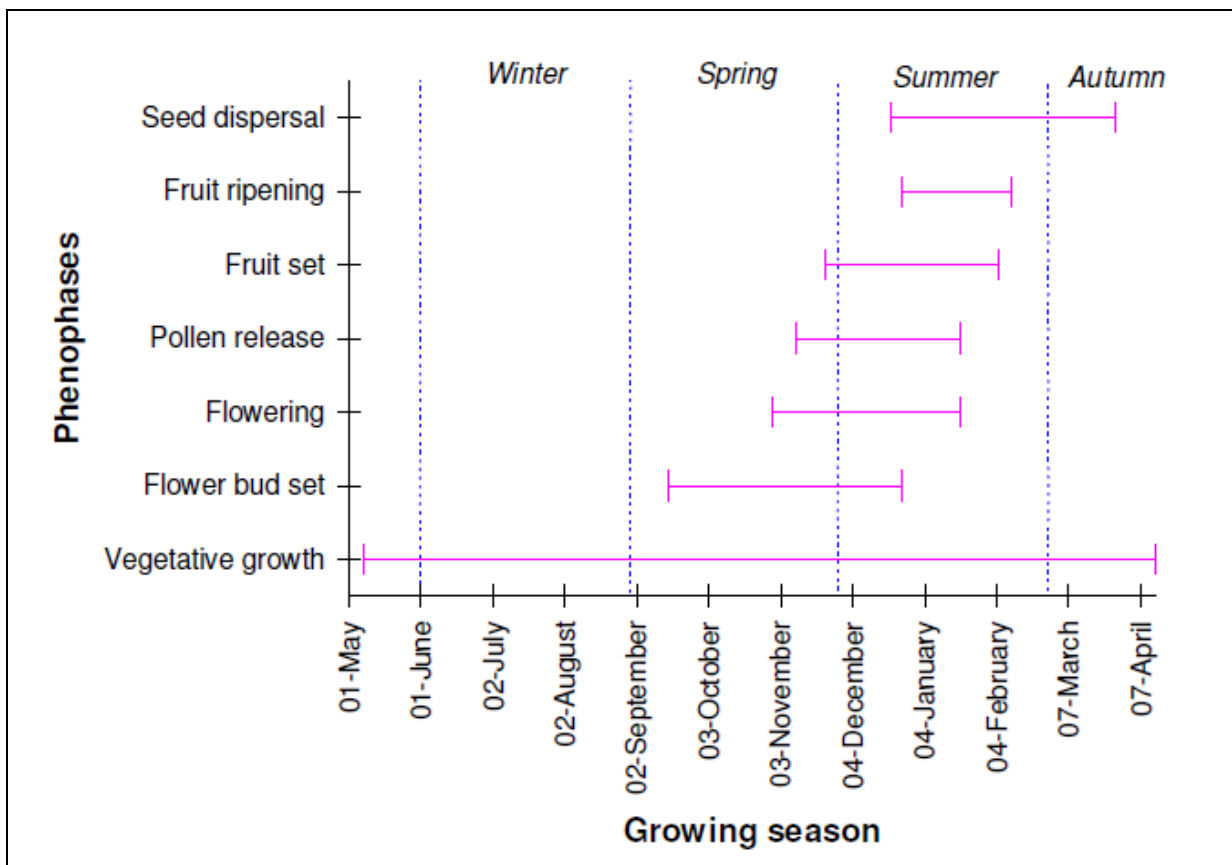
As expected, the species idiosyncratic sensitivity to daylength resulted in phenological variations among species i.e. in phenophase onset, duration and peak occurrence date, as is true of other species (Castro-Díez *et al.*, 2003; Bolmgren & Cowan, 2008; Iversen *et al.*, 2009). Nonetheless, a distinct homogenous species grouping (early, middle and late phenology species) was identified during the onset of flower buds, flowering and seed dispersal. The early (*C. fontanum*, *P. antiscorbutica*, *P. cookii*, *Ac. magellanica*, *A. selago*), intermediate (*C. plumosa*, *C. antarctica*, *R. acetosella*, *U. compacta*, *R. biternatus*, *C. moschata* and *M. fontana*) and late (*Ag. magellanica* and *J. effusus*) budding species was discernible. These homogenous species groupings also remained unchanged during flowering onset except for *C. plumosa* and *C. antarctica* which switched to early group. As for the seed dispersal timing, the pattern was not consistent with that of the flower bud and flowering onset homogenous groupings, except for *Ac. magellanica* and *Ag. magellanica* which remained in the early and late groups, respectively. These distinct homogenous groupings suggest that, within each group, there are no significant differences in optimum daylength that species

require to initiate a phenophase or that species within a group possess similar resource acquisition and allocation capabilities (see also Castro-Diez *et al.*, 2003; Golluscio *et al.*, 2005; Iversen *et al.*, 2009). Conversely, for the timing of other phenophases (pollen release, fruit set and fruit ripening), and phenophase duration and peak occurrence date, no homogenous groupings could be identified.

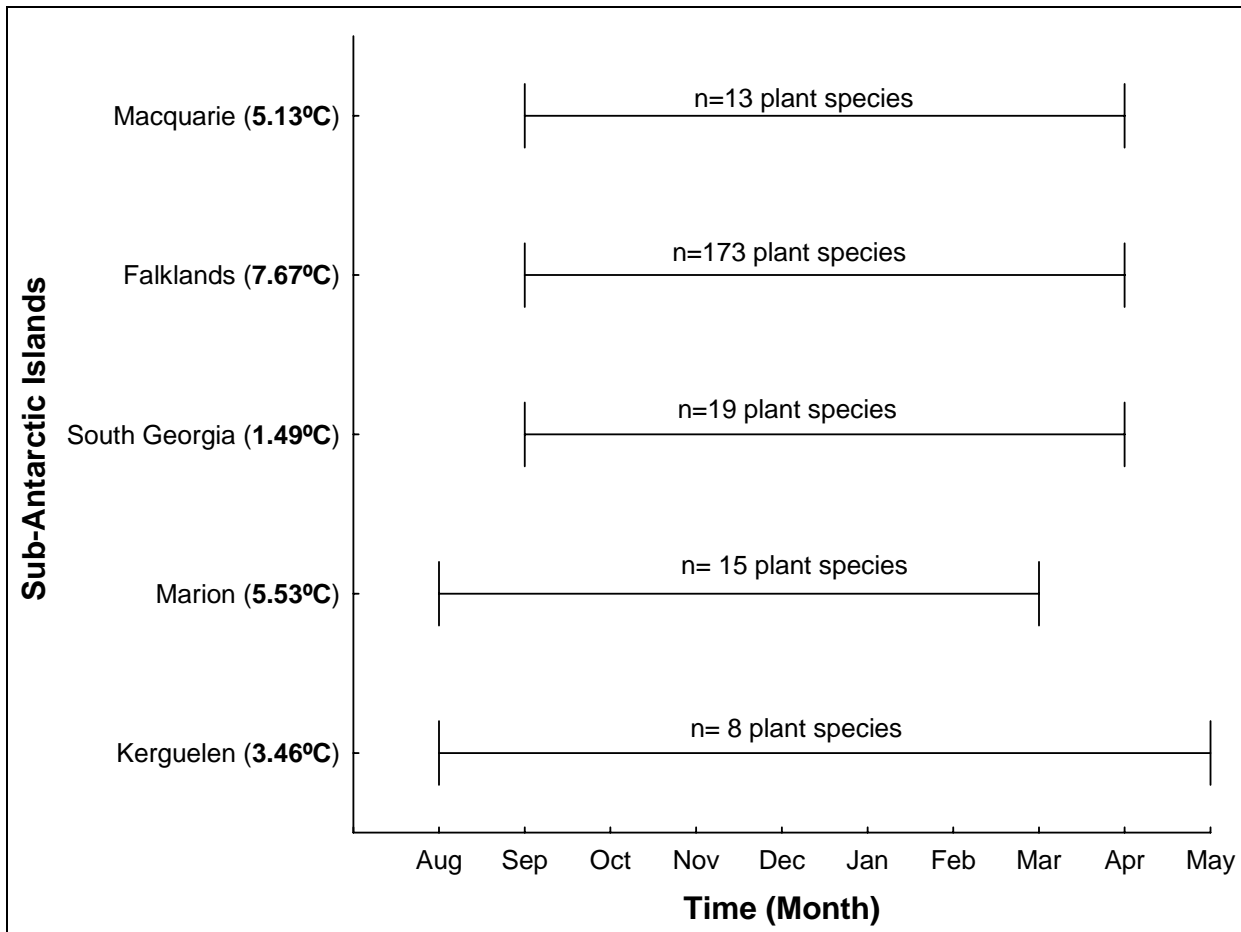
Generally, alien plant species could not be separated from indigenous species. Although its peak reproduction occurred in summer months, *C. fontanum* also reproduced outside the reproduction window of the entire indigenous species complement (beyond spring-summer). As expected, an alien plant may be advantaged by such generalist responses by comparison with indigenous plant species (Meyer, 1998; Daehler, 2003; Godoy *et al.*, 2009), hence its success on the island (Gremmen, 1975; Ramaswiela *et al.*, in preparation). These results imply that *C. fontanum* will further expand its distribution across the island at the expense of indigenous plant species (Byers *et al.* 2002). The two alien plant species, *Juncus effusus* and *Rumex acetosella*, which had similar reproductive seasonality with indigenous plant species have coincidentally shown no signs of colonizing other areas despite their long residence time on the island (Bergstrom & Smith, 1990; Ramaswiela *et al.*, in preparation). Currently these two alien plant species do not pose any danger to indigenous plant species on the island. However, as climate continues to change *R. acetosella* may become a concern since it has an ability to produce abundant, light seeds.

As observed elsewhere, climate change alters the seasonal behaviour of species (Rosenzweig *et al.*, 2008; Miller-Rushing & Primack, 2008; Hülber *et al.*, 2010). In this study, the phenological responses of plants to climate change were species-specific and/or phenophase-specific (i.e. unchanged, delayed and advanced), although majority of the plant species substantially delayed their phenology. The pattern of significantly later phenological developments contradicts those observed in other systems where temperature is typically limiting (Ahas *et al.*, 2002; Amano *et al.*, 2010; Streitfert & Grunhage, 2010). Surprisingly, species reproductive phenologies on Marion Island seem to have responded less to climate change relative to their altitudinal distribution response on the same island (le Roux & McGeoch, 2008). On average, indigenous vascular plant species expanded their ranges upslope in altitude by 69 m (le Roux & McGeoch, 2008) and this is inline with global trends. However, despite the limiting nature of temperature on sub-Antarctic region plant species (e.g. le Roux & McGeoch, 2008), the species seasonal behaviour is daylength cued perhaps due to the aseasonality of temperature (see Chapter 2). For this reason, the substantial phenological changes detected here cannot be attributed primarily and exclusively to warming on

the island as daylength plant sensitivity prohibits too early or late floral induction even in warmer than typical springs (Corbesier *et al.*, 1996; Keller & Körner, 2003; Thuiller, 2007). Probably, these changes might have stemmed from the recording discrepancy from the reference study, sampling frequency and/or phenophase definition differences between historical and current studies (see Chapter 3). Correcting for sampling differences did little to change the flowering and fruit ripening response direction, but in the case of pollen release phenophase some species changed their phenological directions. Indeed these discrepancies are problematic and it is therefore still not clear if the indigenous plant species on Marion Island have shifted their phenology over time. Further work still needs to be undertaken using the current records as baseline information. In conclusion, the research presented here improves the understanding of vegetation dynamics and its drivers. Furthermore the study could be used as a basis for noting the impact of climate change. Doing so would require a sustained programme of systematic sampling on a regular basis – perhaps once every few years over a prolonged time (> 20 year period).

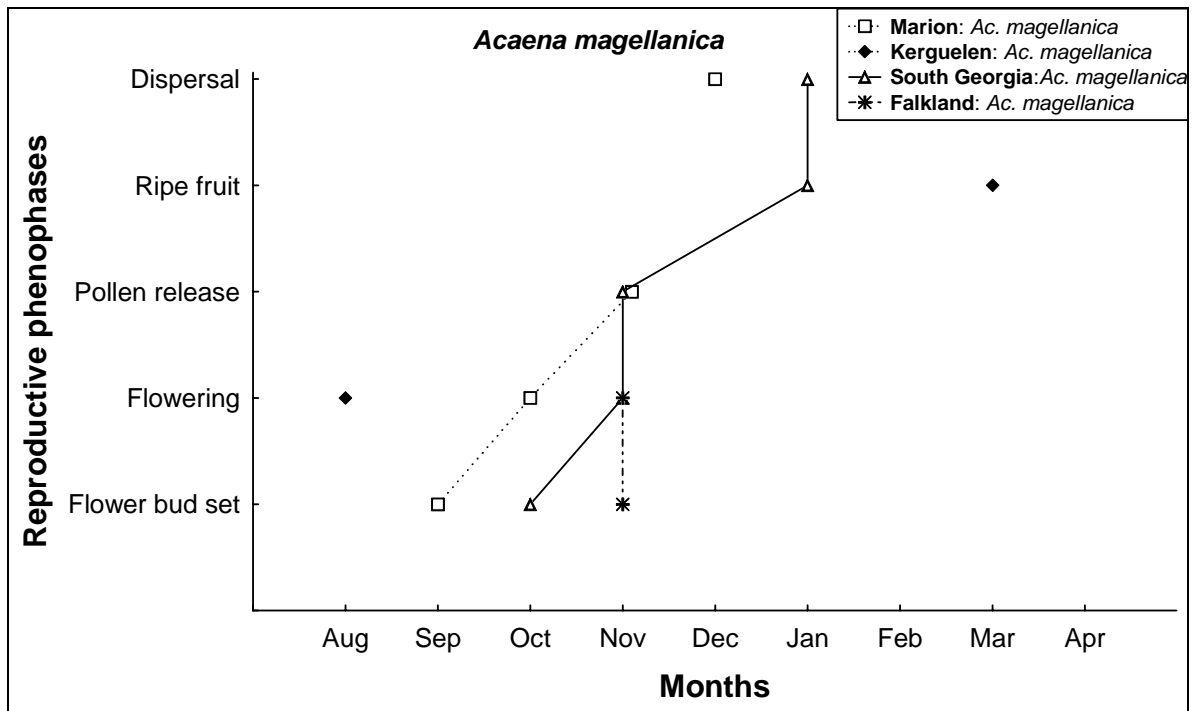


**Fig. 1:** The range of mean first occurrence dates of all phenophases across spring and summer for all of the flowering species surveyed on Marion Island. Dotted lines indicate austral seasons.

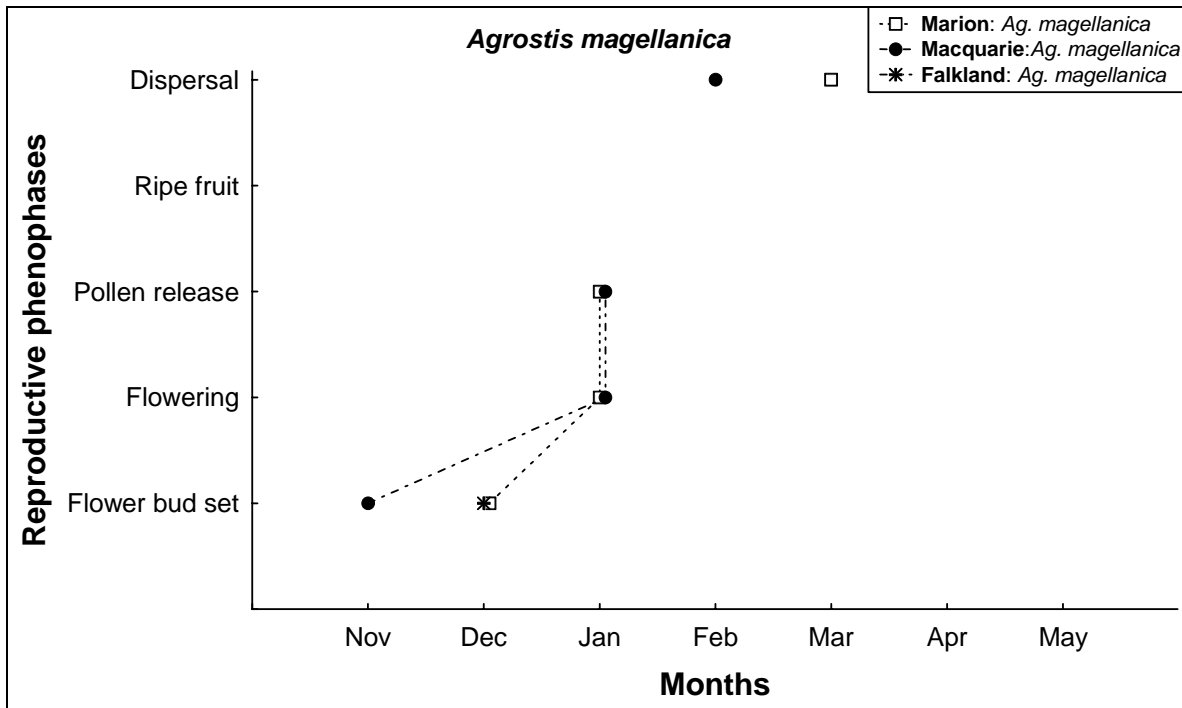


**Fig 2.** The duration of reproductive season in sub-Antarctic region, determined from the absolute timing of first and the last components of reproduction across all species i.e. the species that flowered first and the last species to disperse seeds. Numbers in parentheses on the y-axis are the mean annual temperatures for each island taken from Chown *et al.* (1998). N= the number of plant species used in determining the reproductive season duration/range on each island. The phenological data were summarized from: Macquarie Island - Walton, 1982 and references therein; Bergstrom *et al.*, 1997; the Falkland Islands - Walton, 1982 and references therein; Broughton & McAdams, 2005 and references therein; South Georgia - Walton, 1977b, 1982; Marion Island – this study, Kerguelen Islands - Dorne, 1977; Walton, 1982 and references therein.

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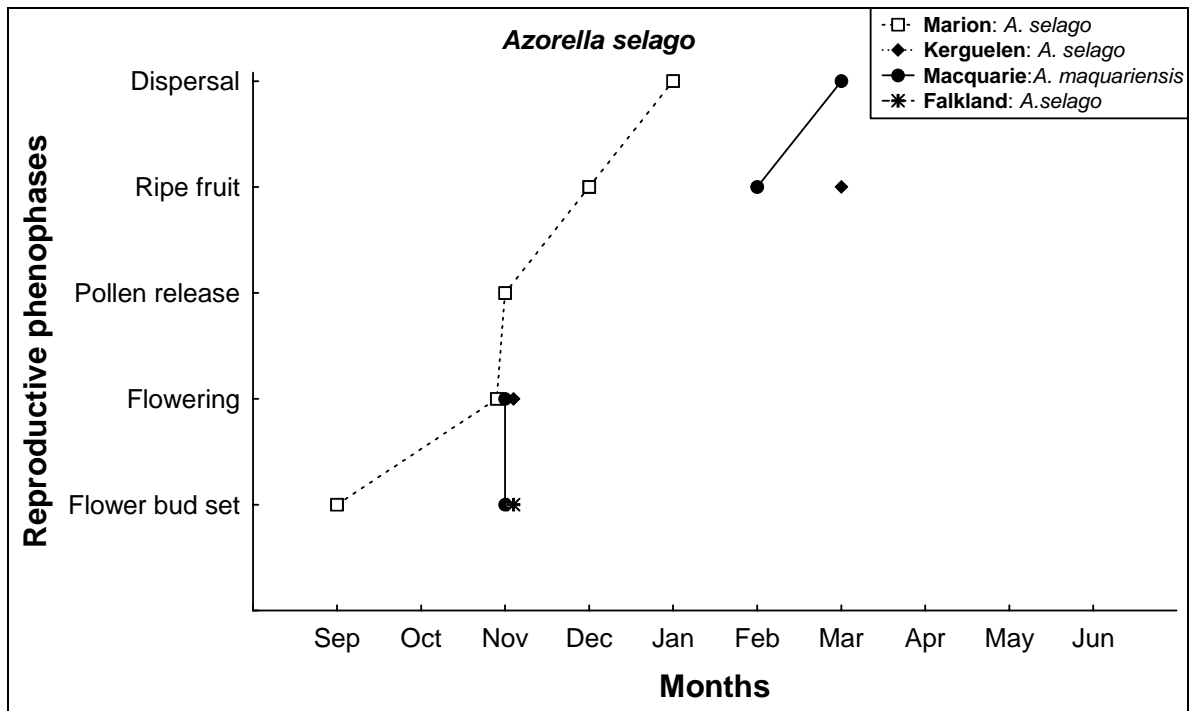


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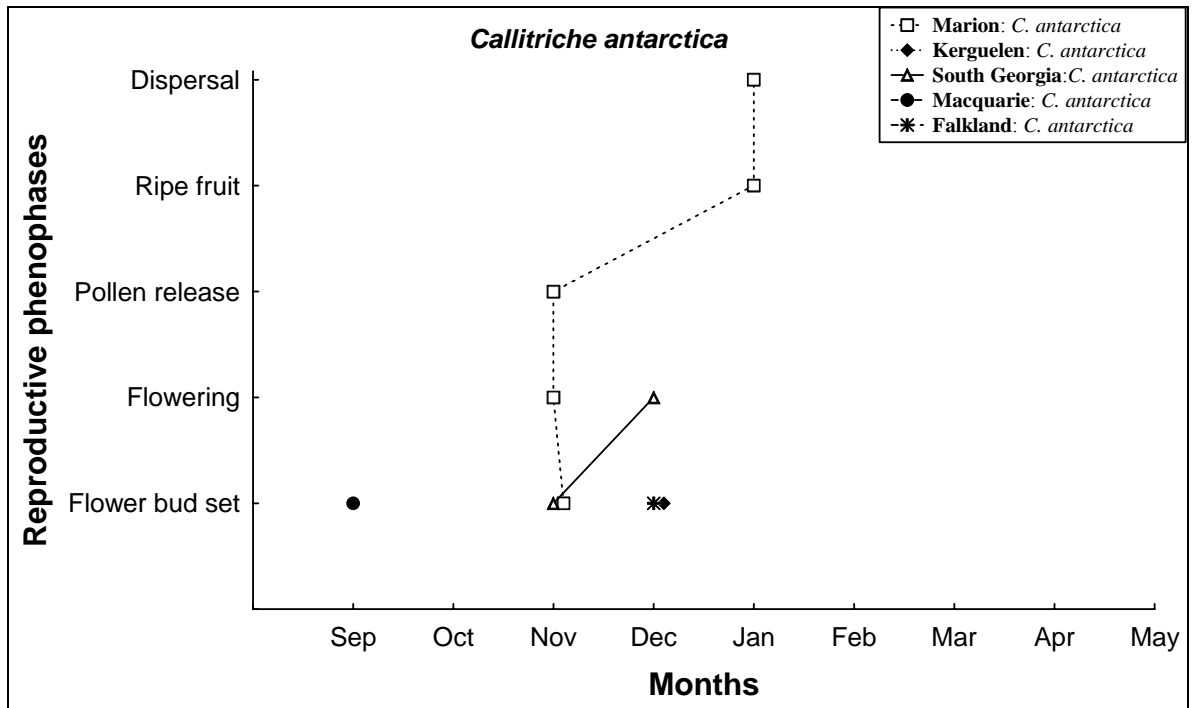


**Fig. 3.** The reproductive phenophases onset date of shared species/genera across the sub-Antarctic region. Y-axis denotes reproductive phenophases and X-axis is the month of phenophase occurrence.

C)

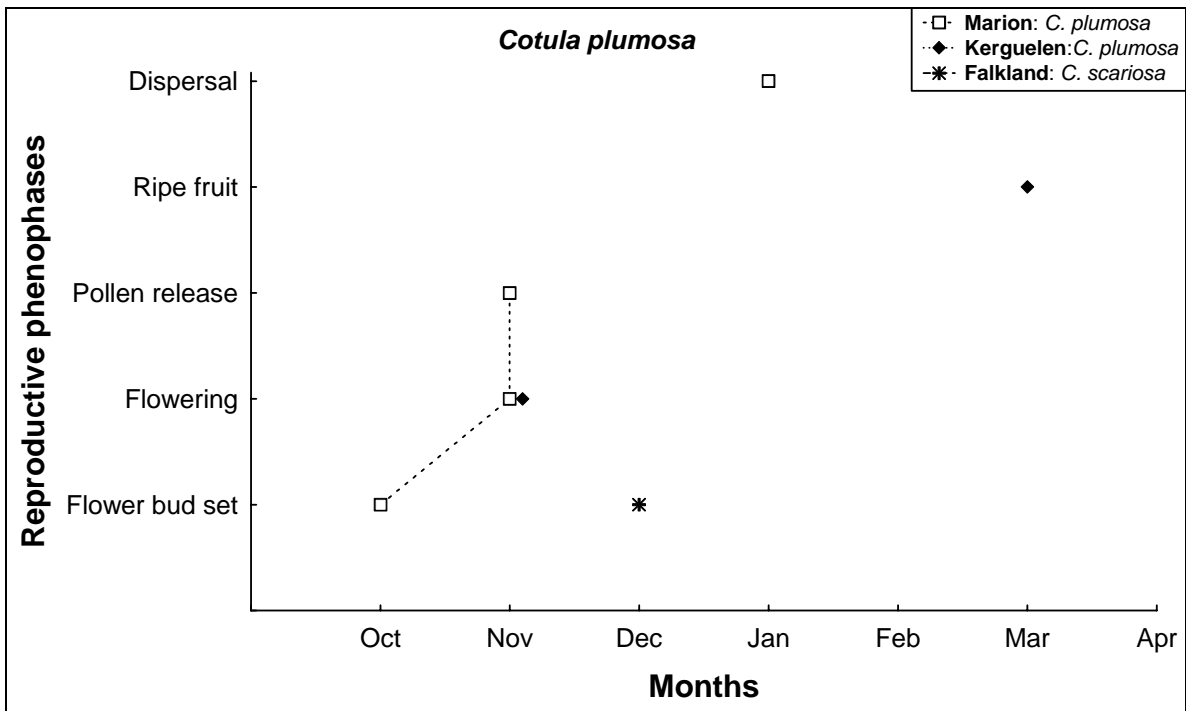


D)

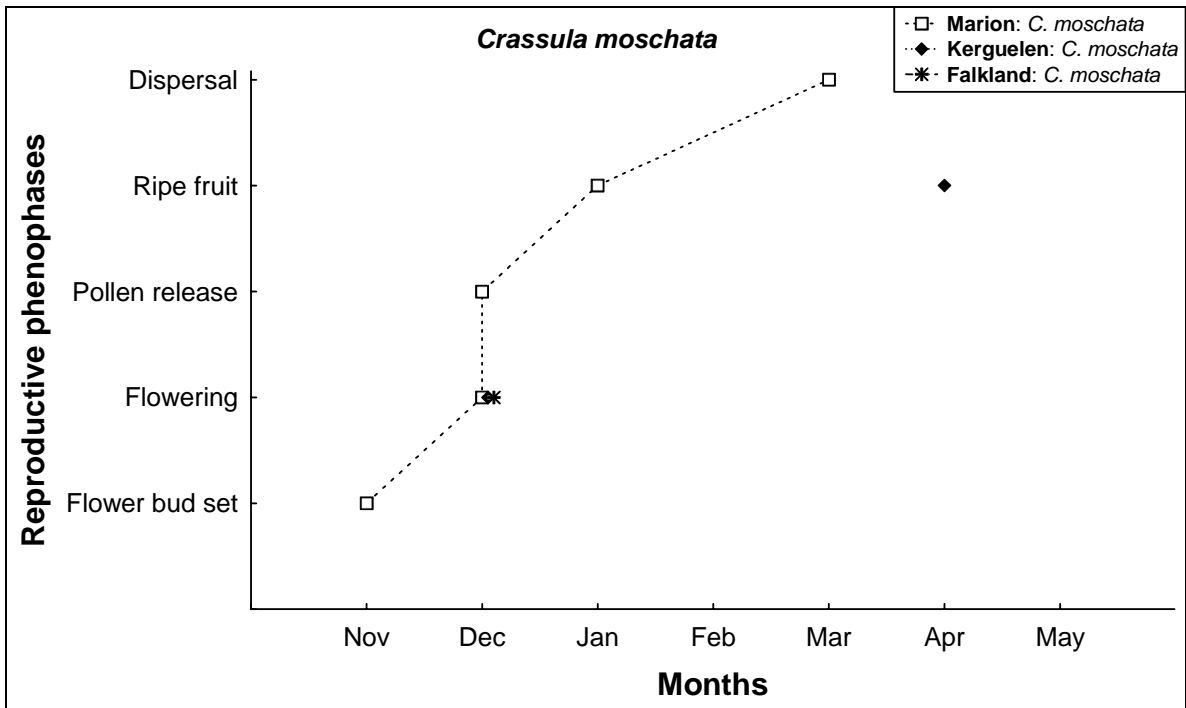


**Fig. 3.** The reproductive phenophases onset date of shared species/genera across the sub-Antarctic region. Y-axis denotes reproductive phenophases and X-axis is the month of phenophase occurrence.

E)

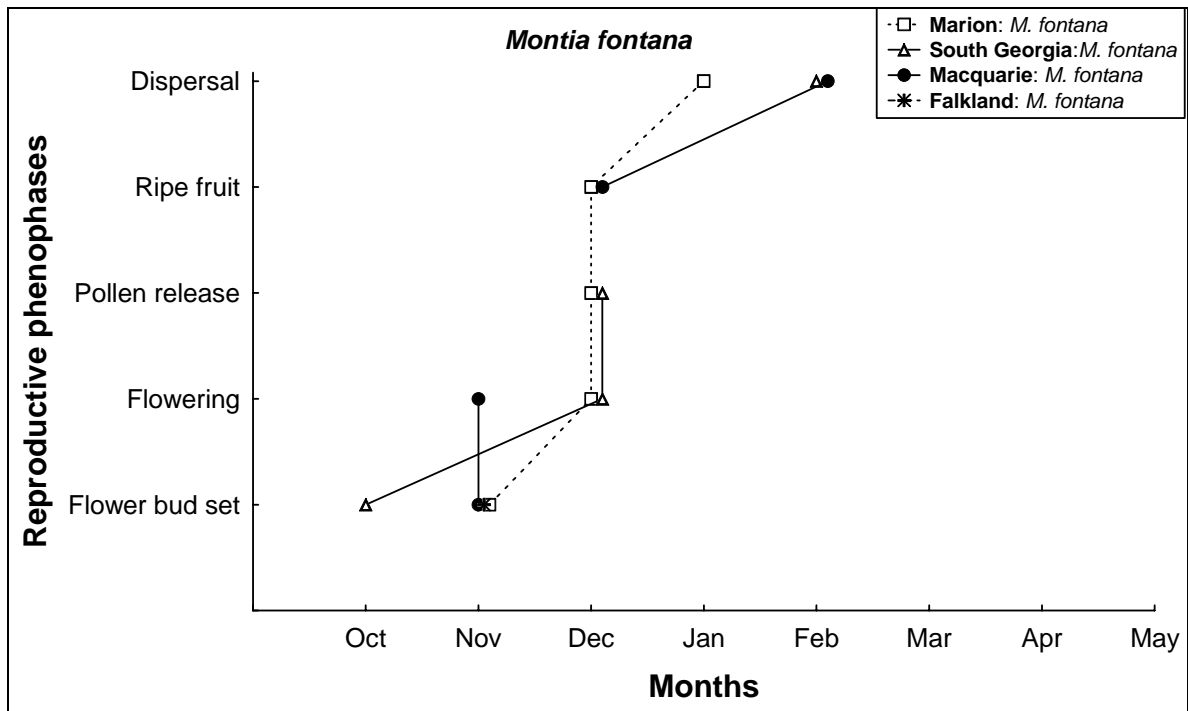


F)

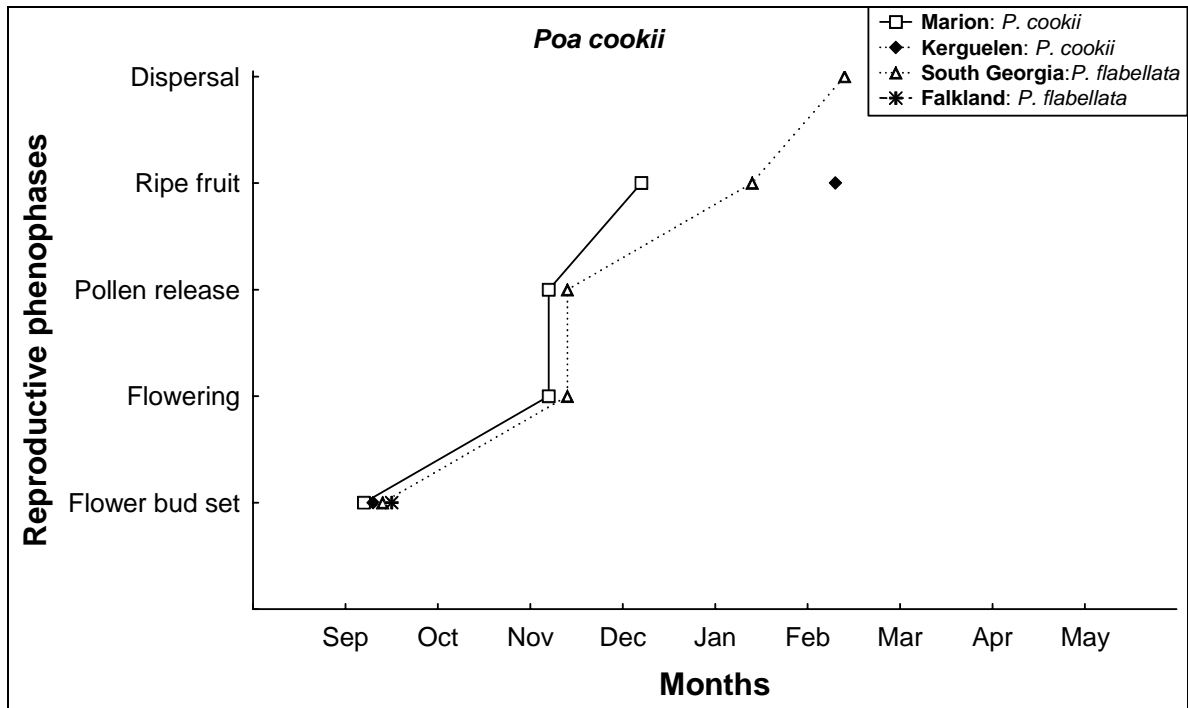


**Fig. 3.** The reproductive phenophases onset date of shared species/genera across the sub-Antarctic region. Y-axis denotes reproductive phenophases and X-axis is the month of phenophase occurrence.

G)



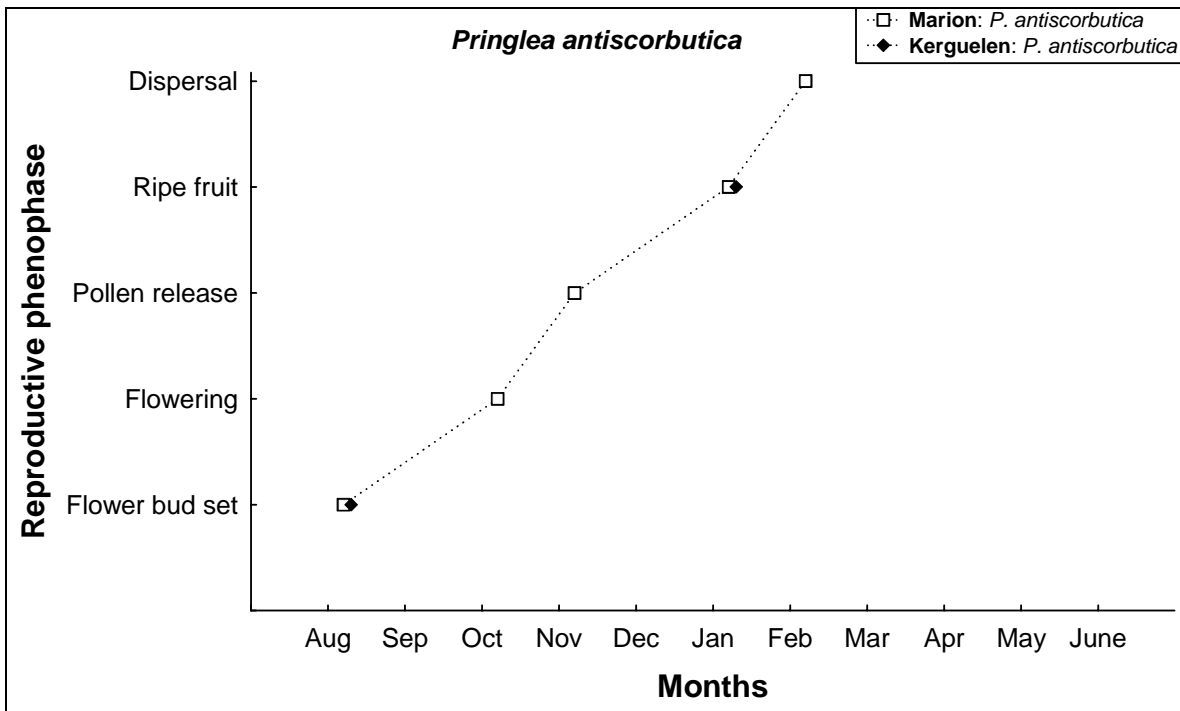
H)



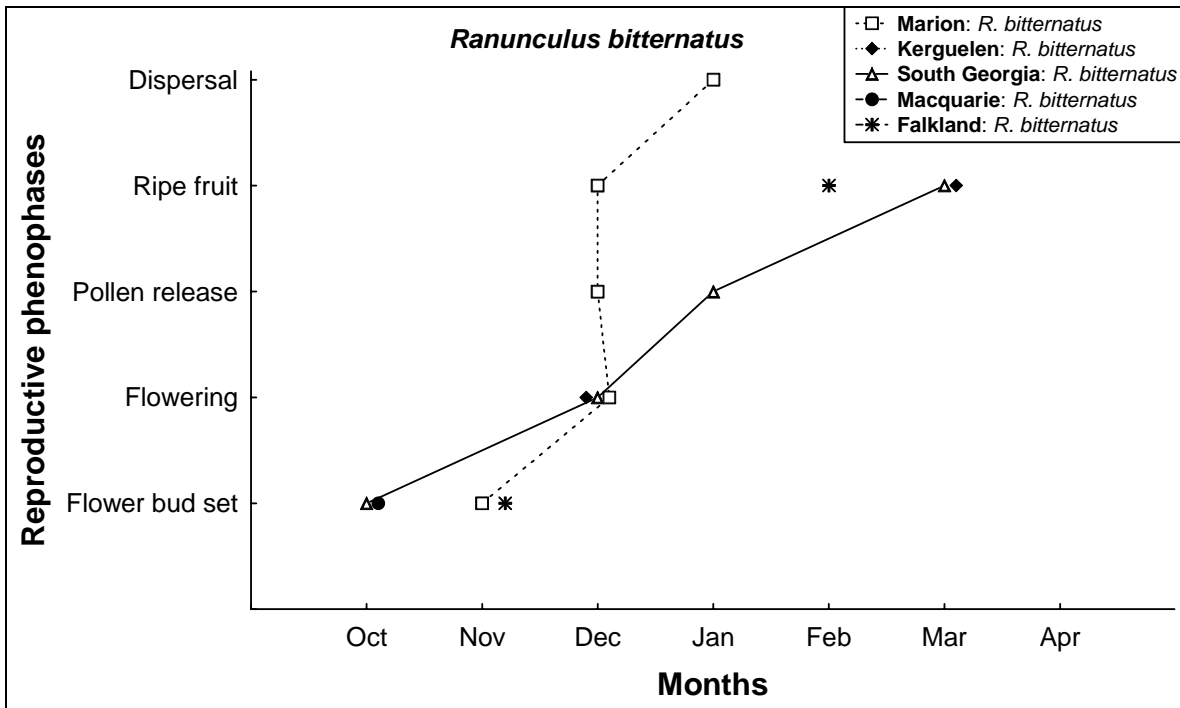
**Fig. 3.** The reproductive phenophases onset date of shared species/genera across the sub-Antarctic region. Y-axis denotes reproductive phenophases and X-axis is the month of phenophase occurrence.



I)

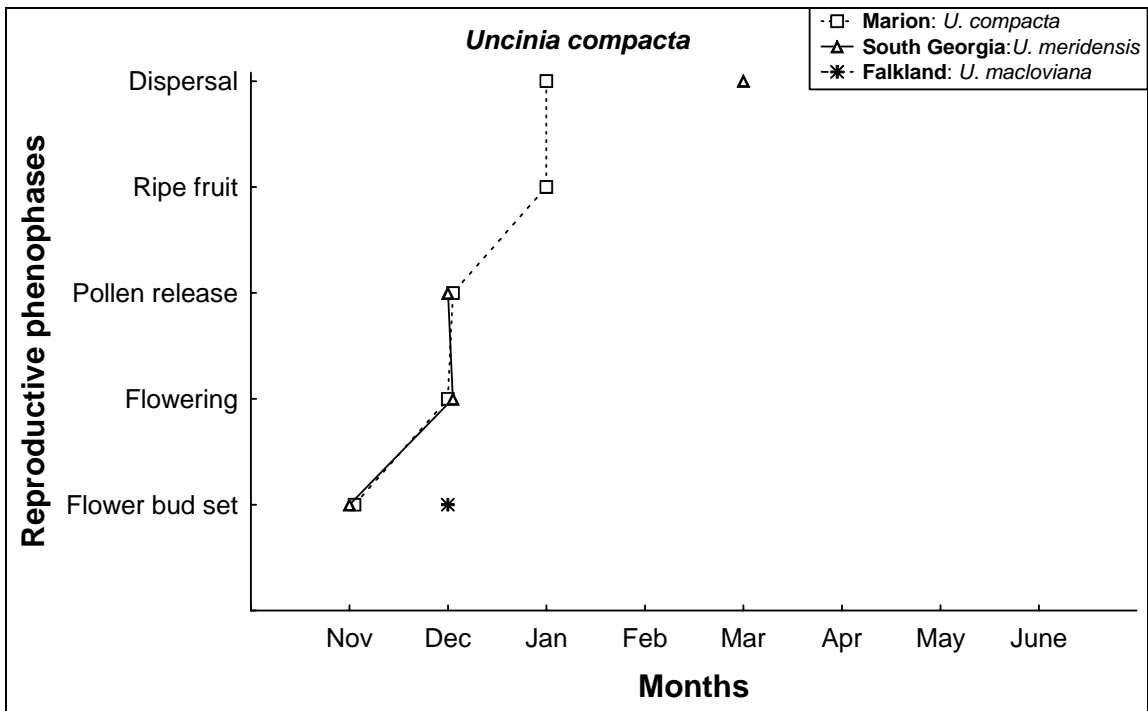


J)



**Fig. 3.** The reproductive phenophases onset date of shared species/genera across the sub-Antarctic region. Y-axis denotes reproductive phenophases and X-axis is the month of phenophase occurrence.

K)



**Fig. 3.** The reproductive phenophases onset date of shared species/genera across the sub-Antarctic region. Y-axis denotes reproductive phenophases and X-axis is the month of phenophase occurrence.

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