

1 **Title:** Putative biotic drivers of plant seasonal phenology: herbivory
2 and pathogens as selective forces, with special reference to
3 deciduousness

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14 **Abstract**

15 Plant phenology is manifested in the seasonal timing of flowering and vegetative processes,
16 but also has ontogenetic aspects. The adaptive basis of seasonal phenology has been
17 considered mainly in terms of climatic drivers. However, some biotic factors as likely
18 evolutionary influences on plants' phenology appear to have been under-researched. Several
19 specific cases of putative biotic factors driving plant phenology are outlined, involving both
20 herbivores and pathogens. These illustrate the diversity of likely interactions rather than any
21 systematic coverage or review. Emphasis is on woody perennials, in which phenology is
22 often most multi-faceted and complicated by the ontogenetic aspect. The timing and duration
23 of shoot flushing may in at least some cases contribute to defences against herbivores, largely
24 through brief periods of 'predator satiation' when plant tissues have highest food value.
25 However, the complete seasonal leaf fall that characterises deciduous plants may be a very
26 important defence against some pathogens. Whether biotic influences drive acquisition or
27 'biotic lock-in' of deciduousness is considered. In one case; of leaf rusts in poplars,
28 countervailing influences of the rusts and climate suggest lock-in. Often, however, biotic and
29 environmental influences likely reinforce each other. Wide re-examination of plant
30 phenology, accommodating the roles of biotic factors and their interplays with environments
31 as additional adaptive drivers, is advocated, towards developing and applying hypotheses that
32 are observationally or experimentally testable.

33 **Introduction**

34 The phenology of an organism is among the key bases of evolutionary adaptation to its
35 habitat. With plants at least, phenology is generally addressed in terms of its seasonal aspect.
36 This involves seasonal timing of growth and reproductive processes, visibly including bud
37 break in spring, shoot elongation, bud set in autumn, natural foliage shedding, production of
38 flower (or strobilus) buds, actual flowering, and development of fruit and eventual fruit drop

or seed shedding. Phenology can also include cryptic features, including initiation of primordia, seed development, timing of cambial activity, the nature of growth rings, and seasonal patterns in root development. Thus, the fullest, most multi-faceted expression tends to be in woody perennials. However, the cryptic phenomena, which include both precursors of and flow-ons from the visible ones, are not addressed specifically here.

The evolutionary drivers of phenology are not only of scientific interest. They are of increasing interest with the accentuated adaptive pressures on plant populations imposed by climate change (e.g. Kijowska-Oberc et al. 2020) and ecosystem fragmentation. Understanding both the evolutionary drivers and the increased pressures will help in future management decisions. An extensive literature on evolutionary drivers of phenology has focused on climates, with their seasonal cycles, the topic being complicated by extreme diversity of adaptive strategies. Numerous trade-offs arise between different features that may contribute to fitness in particular environments. Adaptive strategies for any organisms are thus highly multidimensional, being characterised by how different features interact with each other to create ecological fitness, and not by any single features. Even within a single habitat, different plant species typically vary widely in their adaptive strategies. This is obvious for co-occurring species that are evergreen or deciduous as the case may be. Less obvious, though, are some specific selective forces that shape individual strategies.

In addition to the seasonal aspect of plant phenology is the ontogenetic aspect which, to give perspective, is now considered briefly here. Plants as they get older and larger undergo maturation, which is manifested in widely varying degrees (Poethig 1990; Zotz et al. 2011). It generally involves acquisition of reproductive competence, which introduces a whole suite of seasonal expression. Vegetatively, there can be a transition from a juvenile habit to a mature one, or in some species a relatively abrupt switch (Zotz et al. 2011). Whatever the case, there can be major changes in gross morphology and tissue anatomy.

64 Radical differences between juvenile and adult habits are cases of heteroblasty, which is
65 common in the New Zealand flora (Greenwood and Atkinson 1977). Even vegetatively,
66 maturation can bring some changes in seasonal phenology, very often in a progressively
67 stronger expression of the seasonal phenology (e.g. Wareing 1958; Norskov-Lauritsen 1963;
68 Burdon 1994).

69 Some consideration has been given interplays between biotic factors and plant
70 phenology. In some extreme cases of ontogenetic phenology, heteroblasty in various New
71 Zealand trees and shrubs has been postulated as a defence against vertebrate herbivory
72 (Greenwood and Atkinson 1977), with the juvenile habit being unrewarding for ground-
73 dwelling browsers or else resilient to browsing damage. Despite controversy, and difficulty of
74 proof because the flightless-bird browsers are extinct, definite support for the postulate has
75 been obtained; in a neighbouring island flora with closely related taxa but historically lacking
76 those birds there is not the same heteroblasty (Greenwood 1992; Burns and Dawson 2009).
77 Other, if less striking cases of heteroblasty conferring defences or resilience against ground-
78 dwelling herbivores include the production of sharp spines on foliage or stems during a
79 juvenile phase. And many other cases surely exist. Also, while only incidentally reported as
80 such, *Eucalyptus nitens* (H.Deane & Maiden) Maiden is a case involving a combination of
81 strong ontogenetic phenology and both herbivory and pathogen attack. This species has major
82 geographic variation in the duration of juvenile foliage production (Pederick 1979). The adult
83 phase is subject to insect herbivory while the juvenile phase is very subject to a foliage
84 disease (Johnson and Wilcox 1989), and provenance variation evidently reflects the
85 comparative selective pressures imposed by insect pests and pathogens in respective habitats.
86 Thus, provenances with persistent juvenile characteristics, while enjoying longer protection
87 against insect herbivory, are vulnerable to foliage disease with warm, humid summers;
88 conversely, those with a brief juvenile phase may be less vulnerable to foliage disease but

more so to insect herbivory. In some other cases, the research focus has been on the seasonal phenology of herbivorous insects adjusting to that of the host plant (e.g. Elzinga et al. 2007; Chuine 2010; Singer and Parmesan 2010). In a context of mammalian herbivory, Benning et al. (2018) cite a case of a plant's reproductive phenology constraining its geographic range.

Both biotic and abiotic selective influences were considered decades ago in reviews focused on plant phenology (Rathcke and Lacey 1985; van Schaik et al. 1993). Recently, in relation to the relative importance of biotic drivers of local adaptation, meta-analyses have been conducted — albeit with no specific focus on phenology — by Hargreaves et al. (2020) for biotic effects in plants only, and Briscoe Runquist et al. (2020) for abiotic and biotic effects in plants and animals. Some trends were detected, notably in biotic influences being more important in tropical than in temperate latitudes. However, results were very heterogeneous and perennial plants were weakly represented. Indeed, despite these considerations, the possible extent and diversity of putative biotic factors as evolutionary drivers of seasonal plant phenology appear to remain under-researched. Such factors represent the main focus of this paper. While some postulated cases are cited from the literature, we offer others. Among postulated cases, involving both herbivores and pathogens, we first consider briefly the timing and synchronicity of both vegetative growth (bud burst, shoot flushing and bud set) and flowering. We then focus strongly on the complete seasonal leaf fall that characterises the deciduous habit, in relation to selective pressures imposed by herbivores and pathogens, and address the evolutionary hurdles facing shifts between the deciduous and evergreen habits. Several other cases of putative biotic drivers are also outlined. Coverage involves mainly woody perennial plants, but two cases with pasture plants are considered, along with one involving various wild herbaceous plants. As such, our coverage serves to illustrate the diversity of likely biotic interactions involving plant phenology, and the need for additional investigation, rather than any attempt at

114 comprehensive or even systematic review. We draw heavily on research familiarity with
115 certain species.

116 **Seasonal timing and synchronicity**

117 Phenology is an expression of how a plant species, or a population therein, adapts to an
118 environment. At the same time, while phenological traits are often both variable and heritable
119 within populations (e.g. Li and Adams 1993; Matziris 1994; Skrøppa and Steffenrem 2019),
120 limits to a species' phenology can still govern its geographic range (Chuine 2010), which of
121 course may be altered by climatic change. However, our focus is on likely drivers of the
122 phenology of populations wherever they are growing, considering vegetative and
123 reproductive aspects separately.

124 *Vegetative aspect*

125 In the seasonal timing of vegetative shoot phenology, there are the obvious climatic drivers,
126 reviewed in detail by Axelrod (1966). A classic feature is timing of bud burst, or flushing.
127 For that, optimal fitness will classically represent some balance between the advantages of
128 flushing as soon as conditions favour growth and the safety of delaying it until after almost
129 all risk of late (spring) frost. While meeting that balance should favour individuals'
130 synchronisation of bud burst and shoot and leaf elongation, close synchronisation, when the
131 tissues are still succulent, also offers protection against herbivores. This can operate through
132 a brief period of 'predator satiation' or 'predator swamping' (cf Emlen 1966; Molles 2002)
133 after which the food value for browsers or other herbivores declines sharply. That decline, by
134 helping to limit the herbivore carrying capacity of an ecosystem, represents a feedback
135 mechanism to reduce browsing pressure and thence fitness value of other defences. Many
136 temperate tree species, including various conifers, have very brief seasons of shoot
137 elongation. Often these seasons seem far shorter than the periods when climatic conditions
138 would permit active growth, classic examples existing among the true firs (*Abies* spp). With

deciduous woody plants, however, any such predator-satiation defence may be incidental to the advantage of quick and complete seasonal restoration of photosynthetic capacity.

However, flushing date can also involve a trade-off in defences between climatic and biotic factors, as with sessile oak (*Quercus petraea* (Matt.) Liebl.) in the Pyrenees mountains (Desprez-Loustau 2010; Dantec et al. 2015). Late flushing is a defence against late spring frosts, whereas early flushing helps protect against oak powdery mildew (caused by *Erysiphe quercicola* Takam. et al.). At higher altitudes, where late frost represents the main adaptive hazard, late-flushing genotypes are favoured. At lower altitudes, which are more conducive to the powdery mildew but less subject to late frosts, early-flushing genotypes are favoured. Indeed, the greatest incidence and severity of disease occur at intermediate altitudes. With the trade-off meaning no closely defined or geographically broad optimum for flushing date, the large tree-to-tree variability in flushing date, especially at lower altitudes (Alberto et al. 2011), is not surprising.

Reproductive aspect

Seasonal synchronisation of flowering, which is often closely linked to vegetative phenology, has several obvious benefits, apart from those incidental to optimal timing with respect to climatic factors. Among the benefits, synchronisation helps assure adequate pollen when the female structures are receptive and, by all occurring early enough, assures sufficient time for fruits and seeds to develop and mature before drought or winter cold disrupt such processes. Also, brief but differentiated flowering seasons can also provide reproductive barriers between species that are interfertile but whose hybrids may not be ecologically fit; however, such barriers have broken down in some eucalypt species grown as exotics where their flowering seasons differ from those in native habitats (Eldridge et al. 1993). This synchrony can mean very seasonal food supplies for animal pollinators, but they can be made good by other, sympatric species having differentiated flowering seasons. A further but probably very

164 incidental benefit of flowering synchrony may be creating a brief superabundance for
165 herbivores, in another ‘predator satiation’ situation (cf Emlen 1966; Molles 2002), but Ims
166 (1990) concluded that for this to operate the reproductive synchrony needs to spread across
167 subpopulation units. Similarly, synchrony may militate against a build-up of pathogens that
168 specialise on reproductive structures.

169 Masting, namely heavy seed production in some years with little or none in between,
170 is a means of alternating between predator satiation and predator avoidance, but it is not
171 actually a seasonal phenomenon, so it is not discussed.

172 *Pre-adaptive relationships?*

173 As indicated above, seasonal timing of phenological events may serve as defence against
174 pathogens through avoidance of infection seasons while the plant is vulnerable. Alternatively,
175 the timing may be a source of vulnerability. This seems evident in some cases of freshly
176 introduced pathogens, rather than in historically co-evolved cases. In the case of Dutch elm
177 disease caused by ascomycete fungi *Ophiostoma* spp, early flushing, while it may involve
178 climatic vulnerability, can evidently avoid the height of the infection season (Ghelardini &
179 Santini 2009). With sudden oak death, caused by *Phytophthora ramorum* Werres et al., host
180 vulnerability has been linked to bud burst and onset of cambial activity in the hosts (Dodd et
181 al. 2008). Similarly, the pathogen *Austropuccinia psidii* (G. Winter) Beenken, a rust affecting
182 a wide range of hosts in the Myrtaceae that has invaded parts of Asia and the Pacific, can
183 only infect actively flushing host tissues (Beresford et al. 2020). In each case, invasive
184 pathogens appear likely to place strong selective pressures on the phenology of naïve host
185 populations and understanding the potential for adaptive responses appears to be a
186 worthwhile area for further investigation.

187 **Deciduous versus evergreen habit**

188 Of special note in phenology is the seasonal complete shedding of foliage that characterizes
 189 the deciduous habit, versus the evergreen habit. This was reviewed by Holttum (1953) for
 190 tropical forests and Axelrod (1966) for temperate forests. These important papers exemplify
 191 most subsequent enquiry on the evolutionary drivers of deciduousness, in pointing to factors
 192 of the abiotic environment. Both postulated that seasonal drought was the original driver,
 193 Axelrod that this habit, having originated during the Cretaceous, was a preadaptation to cold
 194 winters that subsequently characterized high-latitude environments along with their
 195 photoperiods. Yet, in many harsh, high-latitude climates, with very severe winters, both
 196 deciduous and evergreen tree species co-occur. Moreover, even within some genera, notably
 197 *Nothofagus* in South America, both deciduous and evergreen species can grow adjacently. In
 198 adaptation to climates with severe winters there are some obvious trade-offs. The deciduous
 199 habit entails heavy seasonal turnover of biomass, but the leaves do not require investment in
 200 anatomical features needed for over-wintering. The habit also allows the leaves to be
 201 photosynthetically very efficient relative to their dry matter (Reich et al. 1992). Apart from
 202 co-occurring species, sometimes close relatives, including both evergreens and deciduous
 203 ones, there are other obstacles to facile climatic interpretation. For instance, deciduousness
 204 exists among many species without severe winters (e.g. Suc 1984; Li et al. 2013). Also, there
 205 are deciduous tropical tree species that produce new foliage well before dry seasons end,
 206 which we will revisit.

207 For the evergreen habit, the anatomical requirements for leaves surviving winters or
 208 other seasonal stresses will tend to make them less attractive or rewarding to herbivores in
 209 general. Such protection against herbivory is very often complemented by toxin production.
 210 All these defences, along with defences against abiotic factors, require additional
 211 investments (Loehle & Namkoong 1987; Strauss et al. 2002; Kursar & Coley 2003; Villar et
 212 al. 2006), or “higher construction costs” (Smith et al. 2019), but such investments can

213 obviate the cost of the complete seasonal turnover of foliage in deciduous plants. Also, early
 214 flushing is not crucial for evergreens to resume photosynthesis in the spring (cf Panchen et
 215 al. 2014). Indeed, Osada (2020) comparing sympatric evergreen and deciduous species
 216 found the former to have later and longer periods of leaf expansion. One might expect
 217 foliage toxicity to be more prevalent and more severe in evergreen species than in deciduous
 218 ones, but we have found no published literature survey on this question. Anecdotally,
 219 however, yews (*Taxus* spp) which are evergreen are both notoriously toxic and often
 220 associates of deciduous species. Within a deciduous example (*Populus deltoides* × *P. nigra*
 221 ‘*Robusta*’) a subtle, seasonal effect of decline in phenolic compounds being associated with
 222 increasing susceptibility to the leaf rust *Melampsora larici-populina* Kleb. was observed by
 223 Maupetit et al. (2018).

224 Unlike much attention given to the energetic costs and associated trade-offs in
 225 alternative strategies of deciduous or evergreen habit, little attention seems to have been
 226 given to the possible roles of pathogens and herbivores in generating or maintaining the
 227 deciduous habit. In relation to the evolutionary pressures imposed by both biotic and abiotic
 228 factors, we consider also the evolutionary hurdles to be overcome in shifting from one habit
 229 to the other. Regarding deciduousness, the presence and life cycles of pathogens may play a
 230 role, and we now consider a probable example.

231 *The poplar rust case*

232 A clue came when two poplar (*Populus*) leaf rusts, caused by *Melampsora medusae* Thum.
 233 and *M. larici-populina*, reached Australia and then New Zealand in 1973 (Van Krayenoord et
 234 al. 1974; Spiers 2007). These fungal pathogens severely affected most of the planted poplar
 235 clones in both countries. Both these rusts spread by urediniospores while the poplar hosts are
 236 in leaf, this spread being polycyclic, but they can produce teliospores on fallen leaves to
 237 overwinter. With severe winters, infection begins from the teliospores and builds up afresh

the next season, although with milder winters some urediniospores from the previous season can germinate to start the build-up. In a co-evolved host/pathogen relationship, this means a comparatively slow build-up of infection during the growing season. However, in New Zealand at least, a semi-evergreen mutant clone of the Lombardy poplar (*Populus nigra* L. cv. *Italica*) had been widely planted, largely as orchard shelterbelts. This had originated in Chile as a somatic mutation. Its widespread presence, with the semi-evergreen habit and the inherent susceptibility to *Melampsora*, very likely exacerbated the initial rust epidemic. The all-year presence of leaves assured a continuous supply of urediniospores, favouring a far quicker build-up of infection in the new season than would be expected from deciduous material. The semi-evergreen clone was very severely affected, presumably with help from a constant supply of urediniospores. The clone was soon almost eradicated, which presumably contributed to the rusts becoming less serious a few years after arriving. Other contributing factors would have included felling of other severely affected cultivars, and a spontaneous proliferation of hyperparasitic and otherwise antagonistic microorganisms in phyllosphere communities on the leaf surfaces (Heather and Chandrashekar 1982).

Admittedly, the poplar/*Melampsora* pathosystem is complicated by *Larix* (larch) being an alternate host for the two *Melampsora* species, which is important for overwintering in severe climates because of the rusts' life-cycle stages on *Larix*. However, this looks unlikely to affect the issue, because of two factors, namely *Larix* itself being deciduous and it not being needed for *Melampsora* to overwinter in mild climates, particularly where a semi-evergreen poplar clone is present to provide a year-round host for the uredinial stage.

Some other possible pathogen influences

Evolutionary pressures imposed by pathogens driving a shift to deciduousness, rather than just maintaining it, are suggested by some deciduous tropical species that produce fresh foliage before a dry season ends (e.g. Borchert and Rivera 2001; Kushwaha et al. 2015). A

specific case is *Faidherbia albida* A. Chev. (apple-ring acacia), a widely distributed, deep-rooting tropical tree species of Africa, found with annual rainfall of 200–500 mm. It flushes vegetatively during the dry season yet sheds its leaves during the rains (Huxley 2001), although it flowers at the end of the wet season. Support for the postulate would come if, when such species are grown with no dry season, the new foliage suffered from pathogens. The success of such a study, however, would depend on the presence of the appropriate pathogens and the triggers for shedding old leaves and producing new ones. An alternative driver, namely increased herbivory pressure during the wet season, seems very unlikely.

Evolutionary barriers to switches of habit

The *Melampsora* story raises two questions: (1) whether the influence of pathogens serves to maintain a habit, or drives switches from one to the other; and (2) if the latter, in what direction? It was long ago proposed (e.g. Holttum 1953; Axelrod 1966) that the deciduous habit arose as a defence against seasonal stresses. But, once established, it may become subject to ‘biotic lock-in’ by factors like the behaviour of *Melampsora* rusts. Answers to both questions, however, depend on the evolutionary hurdles facing the respective switches.

The evolutionary hurdles for a shift in habit will differ between the directions of switch. A related question is what factors, in what combinations, may either drive a switch or prevent one? Another question involves relationships between individual fitness and population fitness. An evolutionary switch from a deciduous to an evergreen habit might be expected to be favoured by a mild climate, imposing no stringent requirements for anatomical and physiological adjustments to abiotic factors. However, it would likely require adjustment to biotic factors. These might include enhanced physical or chemical defences against herbivores, or evolution of greater pathogen resistance. A mild climate, if humid, is likely to favour various fungal or oomycete pathogens, creating a need for greater resistance. Thus, an evolutionary inertia may work against a switch to an evergreen habit.

288 In a co-adapted relationship between an evergreen host and a pathogen, the likely
289 gains from becoming deciduous in avoiding infection pressure appear minor, especially
290 compared with the selective and energetic costs of acquiring the habit. With a new pathogen
291 arriving, the comparative fitness advantages and selective costs can change radically, as with
292 *Melampsora*. This risk is much elevated by increasing human influences, from long-distance
293 trade and travel.

294 *Individual and population fitness and some ramifications*

295 Relationships between individual and population fitness in this connection can be
296 problematic. Classically, population fitness depends on the amount of heritable variation for
297 the trait(s) in question, in the poplar case pathogen resistance and timing of seasonal growth ,
298 and the scope for genetic selection to operate. Thus, the impact of some ill-adapted
299 segregants can be outweighed by a concurrent incidence of segregants that excel their
300 parents' fitness, the latter contributing disproportionately to the parentage of the following
301 generation. However, with pathogens involved, population fitness can be complicated by the
302 nature of infection processes. With a 'polycyclic' pathogen, there can be both reinfection from
303 within the host individual and cross-infection between individuals. For instance, where
304 pathogens impair fitness, an individual becoming deciduous gains little or no protection if the
305 population remains evergreen and can thereby provide an uninterrupted supply of inoculum.
306 In this way becoming deciduous is unlikely to be advantageous unless this results in
307 asynchrony between the window of host susceptibility and presence of inoculum or
308 individuals are too sparse to favour cross-infection. An individual becoming evergreen,
309 however, might impair the fitness of the rest of the population through producing an
310 uninterrupted supply of inoculum, unless it suffers worse than the rest through internal
311 reinfection to become subject to selective elimination. To meet that condition, internal

312 reinfection would presumably need to predominate strongly over cross-infection between
313 individuals, which is likely to be common with polycyclic infection.
314 Becoming evergreen could require evolution of enhanced pathogen resistance and/or some
315 more direct fitness advantage of the habit. Natural selection for resistance may be limited by
316 ‘selective opportunity cost’ whereby the fitness gains from additional resistance are in trade-
317 off with the fitness gains from responses to other selective pressures, some of those gains
318 making good the decay of non-additive genetic components of fitness that occurs upon sexual
319 reproduction. Given the dynamic nature of biotic interactions, along with pathogen mutations,
320 natural selection for ecological fitness can be expected to entail a “red queen” model (Van
321 Valen 1973) requiring endless genetic shifts to maintain fitness. With long-lived perennials,
322 however, such shifts may occur most readily within generational cohorts, during lifespans.

323 **Other putative biotic drivers of phenology**

324 *Swiss needle cast and Douglas-fir*

325 With dates of spring bud burst, populations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.)
326 Franco show a coast-to-inland gradient from the Pacific coast. At a given elevation bud burst
327 comes earlier the further from the coast (Campbell and Sugano 1979), not only *in situ* but
328 also in common-garden experiments, ruling out a simple effect of cooler coastal temperatures
329 caused by the cold ocean current. One possible reason is that coastal populations have a
330 longer humid season in which to complete vegetative growth and cone ripening, especially
331 compared with more easterly populations where summer drought starts earlier (cf Campbell
332 and Sorensen 1978). Another possible factor may be less insolation early in spring. Both
333 factors might reduce the advantages of early bud burst. Another possibility, not mutually
334 exclusive, is that later bud burst escapes the worst of the seasonal hazard, created by
335 humidity, of infection by foliage pathogens. Of such pathogens the most prominent is

336 *Phaeocryptopus gaeumannii* (T.Rohde) Petrak, cause of Swiss needle cast (Boyce 1940;
 337 Mulvey et al. 2013), which is most aggressive in the humid coastal climates.

338 *Two Pinus species and pathogens*

339 Two closely related coastal California pine species are *Pinus radiata* D.Don (either Monterey
 340 or radiata pine) and *P. muricata* D.Don (bishop or muricata pine). They have overlapping
 341 (but almost entirely allopatric) geographic distributions. Of them, *P. radiata* has a very long,
 342 opportunistic growing season, being able to make growth all year if temperatures permit,
 343 which evidently accounts for a very fast growth potential (e.g. Burdon 2001; Burdon et al.
 344 2017). By comparison, *P. muricata* makes minimal shoot elongation during winter, with
 345 apical buds remaining sealed, and is slower growing.

346 When grown in the British Isles *P. radiata* is very prone to a disorder called
 347 “yellows” (Lally and Thompson 2000; Fennessy et al. 2012). This is very severe needle cast,
 348 which was eventually linked to the fungus *Cyclaneusma minus* (Butin) DiCosmo after
 349 problems with false negative isolations. The disease occurs after long spells of mild cloudy
 350 weather in winter and early spring which mean very low insolation at such latitudes. Similar
 351 needle casts have occurred in New Zealand, associated with prolonged very wet and mild
 352 winter weather. These needle casts have been attributed to *C. minus* emerging from latent
 353 pathogen status to cause “spring needle cast” in New Zealand, and to the oomycetes
 354 *Phytophthora pluvialis* Reeser, Sutton & Hansen and *P. kernoviae* Brasier, Beales & S.A.
 355 Kirk (both associated with “red needle cast”) (Fraser et al. 2020). Such weather, with
 356 temperatures allowing growth but with low insolation restricting photosynthesis, is likely to
 357 deplete the carbohydrate reserves that would help the host resist pathogens. By comparison,
 358 the more winter-dormant Guadalupe Island provenance of *Pinus radiata* is less prone to
 359 yellows (Fennessy et al. 2012) than cultivated stocks of mainland California origin. Also,
 360 northern populations (Lat. >38°N in California) of *P. muricata*, which is much more winter-

dormant, are far less prone to such needle casts. While this comparison involves both species as exotics, rather than in natural habitats, it suggests that pathogen pressure can favour winter quiescence despite winter temperatures that permit active growth. That said, *P. radiata* must suffer very severe needle cast before it is outgrown by *P. muricata* (Ades et al. 1992; Burdon and Low 2020). In the northern populations of *P. muricata*, however, selective pressures imposed by such foliage pathogens may have favoured winter dormancy. Winter cold in their coastal environments seems unlikely to be a strong selective force, especially as *P. radiata* (of origin 36¹/₂–37°N) is notable for growing-season frost tolerance (ca - 6°C), which exceeds that of material derived from one such *P. muricata* population (Lat. 39–39¹/₂°N) (Menzies & Holden 1981).

A prominent shoot pathogen affecting pines within and beyond the natural ranges of *P. radiata* and *P. muricata* is *Endocronartium harknessii* (J.P. Moore) Hirats. which causes western gall rust (Old 1981; Ramsfield et al. 2007). It infects soft, elongating shoots during spring to early summer. In certain years, when cool, moist conditions persist during the infection season, abundant infection can occur, giving rise to ‘wave year’ infection. We suggest that the late flushing in the northern populations of *P. muricata*, while it may reduce growth potential, reduces exposure to infection hazard, in a trade-off. By comparison *P. radiata*, with its earlier shoot flushing, is vulnerable to infection over a longer season, although the dryer habitats south of San Francisco Bay mean that infection hazard is lower. The fitness advantage of the greater growth potential of *P. radiata* resulting from the longer growing season, maybe with some enhanced genetic resistance, evidently outweighs the fitness cost of the associated extension of the infection season in its habitat. The fitness cost of susceptibility is likely mitigated by susceptibility being largely confined to young trees (Old et al. 1986) which often arise at high density from stand-replacing fires, with mortality from the gall rust representing essentially soft selection.

There is thus reason to suspect that both foliage pathogens and western gall rust have imposed selective pressures contributing to the comparative seasonal phenology of *P. radiata* and northern populations of *P. muricata*. Problematically, however, this interpretation does not account for the southern populations of *P. muricata* (<37°N) also showing later flushing and pollination than *P. radiata*, although those populations do so earlier than the northern populations (Brown 1966). (These populations are acutely susceptible to foliage disease (Ades et al. 1992; Burdon and Low 2020) but are naturally exposed to low disease hazard.) Brown studied pollination dates, which would be a reliable proxy for comparative flushing dates, in an essentially common-garden situation near Canberra. There is only one location, Monterey, where the two species naturally co-occur, and different pollination dates are putatively an adaptive crossing barrier there. Later pollination in other southern populations of *P. muricata* is not so readily explained, although it did not closely fit a clinal pattern. Moreover, the cool site near Canberra may have distorted the comparative phenology of the southern populations.

Pathogen-induced stimulations of phenology

As well as putative cases of pathogens operating as selective influences on seasonal phenology, pathogens can exert more direct phenotypic effects on phenomena that belong within the underlying seasonal phenology of the hosts. Classically, foliage infection is a widespread cause of premature leaf fall. Such cases generally entail hosts responding to infection by abscission of foliage or foliage structures. The responses can be adaptively significant, as defence mechanisms for the hosts (Fraser et al. 2016). In some cases, shedding infected foliage may remove inoculum, as well as possibly denying a pathogen further sustenance. This appears to be so in the case (already mentioned) of needle cast associated with *Cyclaneusma minus* in pine species. In some other cases, prompt shedding of foliage can prevent dangerous spread of the pathogen within the host. With white pine blister rust, caused

411 by *Cronartium ribicola* J.C.Fisch, abscission of fascicles can serve as an effective resistance
 412 mechanism in both *Pinus monticola* Douglas ex D.Don (Hoff & McDonald 1971) and *P.*
 413 *armandii* Franch (Hoff & McDonald 1975). While infection-related foliage abscission
 414 typically shows seasonality governed by infection and/or sporulation cycles of the pathogens,
 415 along with seasonal fluctuations in the host's carbon economy, this does not mean that the
 416 abscission is intrinsic to the host's seasonal phenology.

417 In contrast to infection-triggered foliage abscission, infection of larch (*Larix*) foliage
 418 by *Hypodermella laricis* Tuboef can stop natural abscission, thereby keeping the foliage as a
 419 continuing source of inoculum (Cohen 1987).

420 *Grazing regimes and pasture plant phenology*

421 Outside forest trees, three cases are adduced for herbaceous plants, two for pasture plants,
 422 and one for a collection of species in a Mediterranean climate. In one pasture-plant case, the
 423 seasonal phenology, seemingly driven by climate, may actually be driven largely by biotic
 424 factors in conjunction with climate. Key aspects of pasture-plant phenology are seasonality of
 425 forage growth and flowering. An extended growing season, with consequent forage
 426 production, is widely sought by breeders. However, there is classically a trade-off between a
 427 long growing season and the persistence that avoids a need for frequent sowings to ensure
 428 sward renewal. Cold tolerance is typically associated, among populations, with level of
 429 winter dormancy, suggesting that active growth is physiologically incompatible with cold
 430 tolerance. Yet Daday (1964) observed otherwise. He studied geographic races of *Medicago*
 431 *sativa* L. (lucerne or alfafa), and found the expected picture of a close association between
 432 level of winter dormancy and cold tolerance, admittedly not with severe winters. But, in the
 433 F2 and F3 generations of an interpopulation diallel cross that association broke down. This
 434 independence of inheritance of the two traits conflicted strongly with accepted doctrine, yet
 435 no attempt to ascertain its underlying evolutionary significance appears to have been

published. We postulate that the observed winter dormancy was in large measure a defence against browsing pressure, which would be intense in winter and very depleting of the plants' resources if they were making active growth, rather than being a directly climatic adaptation. With severe winters, however, dormancy would likely be physiologically obligate, but that would not preclude breeding to extend autumn growth (Castonguay et al. 2006).

In the other case involving pasture planes, namely forage grasses, a biotic driver of phenology has, however, been long recognized, at least implicitly. Late and brief seasonal seed-head formation is a feature of persistent 'pasture type' strains with ancestral history of adaptation to intense grazing (e.g. Charles 1961).

Much more recently, Waterton and Cleland (2016) studied six local and six non-local plant species grown in a common Californian Mediterranean climate where two species of rabbit applied herbivory pressure. In the absence of the herbivores early seasonal commencement of growth (shown by the non-local species) conferred a productivity advantage, but with herbivory delayed commencement was associated with an advantage. Thus, a delay was evidently a defence against herbivory, in a classic trade-off between defences and growth potential (cf Loehle & Namkoong 1987; Strauss et al. 2002).

Concluding

How a situation plays out will depend on many factors, including: the general climatic context and the constraints it imposes (along with other environmental factors); the nature of biotic pressures, viz herbivory, pathogens; the reproductive biology of pathogens including seasonality; the host plant ecology, in the scale from highly gregarious to essentially solitary; and the genetic systems of both host and pathogens. Not to be ignored are interactions with other plants in the ecosystem and among herbivores.

Influences of climate are both direct and indirect, the latter category involving herbivores and pathogens. With pathogens, there is the classic 'triangle' of interactions

involving host, pathogen and the environment, so the direct and indirect influences are in some degree interdependent. With the poplar/*Melampsora* pathosystem, where a direct influence of climate may favour an evergreen habit, the indirect influence, through the effect of the same climate on the pathogen, is likely to militate against that shift. Often, however, the evolutionary pressures from climatic and biotic factors would be mutually reinforcing, as in the *Medicago* case.

In calling for a broad evaluation of biotic factors as evolutionary drivers (or co-drivers) of plant phenology, the coverage is preliminary and selective, representing an alert to the topic. Even a systematic literature review would still require interpretation of individual cases. Challenges certainly exist in such evaluation. To identify likely cases of biotic drivers, we must look largely to those who know intimately individual plant species and their ecology. Then detailed review and analysis of available evidence is needed, but interpretation in individual cases may still be problematic. From there, the general postulate of biotic influences will need to be carried forward into hypotheses that are observationally or experimentally testable.

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672 RDB drafted the manuscript and made final revisions, and MJB contributed revision and
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