

Flowering Phenology: An Example of Relaxation of Natural Selection?

J. Ollerton and A.J. Lack

Flowering phenology has normally been viewed as fundamental to a plant species' reproductive ecology. Researchers in the field have emphasized the adaptive importance of flowering at a particular time relative to other individuals in the population, or other species in the community. An alternative view, however, is that flowering phenology is a trait that may not be under strong selection, and this may have allowed some variation to appear in populations by chance.

Arguments about the relative importance of natural selection versus nonselective factors, such as chance colonization and genetic drift, continue to flow through many aspects of plant ecology. In studies on the regulation of plant populations, it has been shown that the most critical stage in many populations is regeneration – specifically, between seed germination and the vegetative establishment of the individual¹. In this, and therefore in the regulation of plant populations generally, it has been convincingly suggested that there is a large density-independent effect in many populations².

The number of individuals produced in any one generation seems to be determined more by external conditions, such as climate, associated vegetation and animal activity, rather than by phenomena intrinsic to the plant population *per se*. Thus, there can be a large element of chance determining exactly which individuals colonize a given area: those that arrive at the right place first have an overwhelming advantage regardless of their relative competitive ability. Under these circumstances there is the potential for an element of non-regulated variation to creep into many plant populations purely by chance. Self-thinning and density-dependent population regulation may well be important in monocultures, or in those plant species that form dominant stands^{3,4}, and in

these situations one can imagine selection to be a more potent force regulating any variation. However, such species may be in the minority.

Against this background of potentially unregulated variation, we focus here on flowering phenology. Not only is this a property of plants that is easy to measure, but also there have been a number of studies within the last 15 years or so that have shown variation either between populations or between individuals within populations⁵⁻⁹.

Above the level of the individual inflorescence or flower, the study of flowering phenology can be readily subdivided into four areas:

(1) Intrinsic, phylogenetic factors affecting phenological patterns on a global scale; the best-known study of this type is that of Kochmer and Handel¹⁰, but see also comments by Primack¹¹ and Grime and Mowforth¹².

(2) Phenological differences between coexisting species; most emphasis has been on closely related (usually intrageneric) taxa^{5,13} but some work has been done on guilds of species which share pollinators¹⁴ and on community patterns¹⁵.

(3) Studies of phenological variation between populations of one species, either along latitudinal or elevational gradients^{16,17} or between ecologically distinct habitats⁵.

(4) Intrapopulation studies of variation in the flowering phenology of coexisting individuals^{18,19}.

The arguments associated with each of these areas are somewhat different, but tend to have a common selectionist flavour. The extent to which this position is justified is debatable.

What exactly is adaptive about flowering phenology...?

It has been demonstrated that particular angiosperm families flower at distinct times of the year¹⁰. That this pattern covers two separate continents, at least, shows that flowering time is a conservative character. Primack¹¹ commented that it may be the time needed for fruit maturation that is the important determinant of when a species flowers, rather than constraints on

flower production, but the fact that flowering phenology is only rarely used as a taxonomic character adds weight to the conclusion of its conservative nature. It has also been shown that the amount of DNA in the cells of plant species is correlated with timing of growth and, frequently, flowering time¹². These studies have demonstrated possible constraints on flowering phenology but have not suggested any particular ecological reason for these trends, nor is it easy to think of one.

A few species have, apparently, lost any constraint on their flowering time. For instance, *Senecio vulgaris* is a largely self-pollinating weed that can flower at any time of the year. Weeds live in an environment in which speed of growth and reproduction will be strongly selected for and flowering time may be somewhat incidental. Most self-pollinating species, like outcrossing species, have a predictable, and often quite short, flowering season. *Senecio vulgaris*, however, has clearly not been constrained by its phylogeny; exceptions such as this need to be carefully studied.

Authors have drawn conflicting conclusions from studies of the flowering phenologies of coexisting species; these plants may compete for pollinators, but usually this is inferred rather than demonstrated, and a number of studies have shown very little competition for pollinators within communities²⁰ or between co-occurring species²¹. Different plant species may, in fact, facilitate each others' pollination by attracting more pollinators to an area because of greater total food reward^{22,23}. It is possible that these situations are adaptive in a coevolutionary sense, but such interactions are hard to tease apart since, usually, any possible 'control' has different conditions associated with it. In many environments there is great variation in pollinating insect diversity and abundance, both among sites and between years^{21,24}; this unpredictability may result in a relaxation of selective forces.

There is often a strong selective argument for the timing of flowering when one examines different populations of one species; for instance, increasing latitude or altitude in north temperate areas can lead to

J. Ollerton and A.J. Lack are at the School of Biological and Molecular Sciences, Oxford Polytechnic, Gipsy Lane, Headington, Oxford, UK OX3 0BP.

progressively later flowering¹⁷, as can changes in other environmental factors¹⁶. Although such shifts in flowering time may sometimes be the result of physiological limitations rather than natural selection, a genetic basis has been demonstrated in some species^{16,17}.

Within one area there can be populations living in habitats that differ in their management. This is clearly seen where there are hay meadows which have been cut regularly during July or August over several centuries: the meadow plants flower earlier than nearby populations of the same species not influenced by this cutting regime⁵. The differences in flowering time between these populations may be as great as two months for some species, leading to the meadow populations flowering at what is otherwise an atypical time of year. In these examples, the differences may be explained easily and convincingly by selection.

Differences between individuals in flowering phenology touch one of the cornerstones of Darwin's original ideas on natural selection: the concept of variation between individuals in the same population. Highly synchronized populations which respond to precise flowering cues and flower over a short space of time have been described, as have populations in which individuals differ in their peak flowering by a number of weeks^{6,13}; these are the extremes of a continuum⁹. The majority of species and populations show some variation in flowering time, although pronounced asynchronous flowering (i.e. differences in peak flowering of the order of weeks rather than days) within a population has been described only for a small number of plant species. Evidence for a genetic basis to the phenomenon is available for some species although not for others⁷.

Augspurger's experimental manipulation of flowering time in the highly synchronous tropical shrub *Hybanthus prunifolius* showed clear disadvantages for individuals flowering asynchronously relative to the rest of the population²⁵. This is interpreted as directional selection acting against variation in time of flowering.

In a number of species, flower-

ing phenology is clearly a variable character, and we suspect that such variation may prove to be more widespread than is presently thought. Interpretation of population flowering phenologies depends in part upon how the data are manipulated and presented graphically: combining the flowering data of individuals to show population trends (a commonly employed technique) may show a flowering peak, but unless there has been an attempt to show the degree of variation large individual differences may be masked. A number of published studies of population flowering phenologies omit this information.

As might be expected, most authors have stressed the interaction between the genetically based characteristics and environmental modifiers, particularly microsite variations in factors such as water regime and soil nutrient concentration. In hypotheses to account for asynchronous flowering within populations, the role of natural selection in promoting or maintaining this variation is usually emphasized. The main hypotheses are as follows^{8,9}:

(1) Reduced intraspecific competition for pollinators⁸.

(2) Pollinators encouraged to move between individuals, increasing outcrossing²⁶.

(3) Increased mate availability if there is no rank correlation of flowering time of individuals between years²⁷.

(4) Reduced seed predation²⁸.

(5) Disruptive selection due to variation in numbers and timing of predation and dispersal⁹.

(6) Differential selection between years, depending on weather⁹.

All of the work published so far on asynchrony of flowering within populations has tried to explain the phenomenon in adaptive terms (and has even tried to describe and quantify the selection in the asynchronous *Senecio integrifolius*²⁹), arguing that the asynchrony exists because of selective forces exerted at some time in the history of the species, and that asynchrony now confers some advantage on the individuals in that population. But is this analysis necessarily correct for all situations?

...and what is neutral?

Those characters that are liable to be under the strongest natural selection are generally of little use taxonomically and do not correlate well with evolutionary affinity except in the broadest terms. Since flowering time has been shown to be strongly associated with evolutionary affinity, then either the developmental constraints on flowering phenology are so great that they override any potential natural selection, or selection on flowering time itself is not a strong evolutionary force.

The latter conclusion is, to some extent, borne out by the fact that there are exceptions to the general flowering period of a family; one can think of examples in any large plant family: in Europe, *Tussilago farfara* and a few other Asteraceae flower early in the year for what is a fundamentally late flowering family. Although flowering time is conservative, natural selection can act to alter it, and one can imagine that there may have been strong selection on these exceptions. The fact that the majority of a family still flowers at a similar time suggests that there has not been strong selection on these plants for a shift in flowering time.

Flowering time does appear to be, at least, a somewhat variable character, but does not normally shift as much as might be expected between species or populations. One factor which has not been fully investigated is the possibility that divergence of flowering time is uncommon because there are other floral attributes which may be more effective in reducing interspecific competition for pollinators⁸. Examples of such traits may be scent, coloration and patterning, size, diurnal opening time, or breeding system. If there is a valid argument here, it may be evidence that flowering time is under relaxed selection relative to other reproductive attributes. It is significant that Rabinowitz *et al.*¹⁵ found an apparently random set of flowering times in 71 outcrossing species in tall grass prairie with no difference between wind- and insect-pollinated species.

If there is some level of asynchrony of flowering in most plant populations, then we may consider synchronous flowering to

be a derived condition, implying strong selection for concurrent flowering. There may be advantages associated with flowering synchrony⁸, but if precise synchrony in flowering is really rare, it suggests to us that the flowering phenology of most species is not under strong selection.

One can, in fact, think of a number of disadvantages to countermand the hypotheses set out to account for asynchronous flowering within populations. For example, if there is a genetic basis to variation in flowering time, closely related plants are likely to be synchronous, leading to potential problems of inbreeding. This would be compounded by the fact that the effective population size may be reduced. Finally, flower or seed predation may be concentrated on a few individuals at a time rather than the effect being diluted over a larger population²⁵, but see Ref. 28.

Thus, do we need to raise selectionist arguments to explain asynchronous flowering within populations? Variation in almost any feature is likely to be thrown up by chance factors. For a perennial plant species, being at a slight disadvantage in terms of seed set in one year over another may be fairly immaterial, particularly if there is little seedling recruitment going on anyway. In many species, although there are differences – consistent genetic differences – in flowering time between plants, each individual plant usually flowers over quite a long period, potentially setting seed throughout its flowering year.

Over a period of years, one can imagine that it would make little difference whether an individual's flowering peak was, say, three weeks

earlier than another. Natural selection is concerned with the lifetime reproductive success of individuals, and if the success of any one flowering type is no better or worse than that of the others, natural selection will not act to synchronize flowering time. Differences in flowering phenology within a population may not need a selective explanation.

Of course, we are not stating that the above scenario applies to all populations, or that asynchronous flowering can never be an adaptive response; there may be a wide range of situations where natural selection acts on a species' flowering pattern. However, rather than always invoking evolutionary solutions to ecological questions, a simpler approach may be to think first in nonadaptive terms.

Natural selection relies upon a complex set of peculiar circumstances, and may not always be involved in maintaining the genetic variability that is a feature of all populations. Flowering time seems to be one character in which variation is often seen but, in many populations, may be under relaxed selection pressure; this allows variation to persist and gives the species potential to evolve if a stronger selective regime is imposed at any time.

There are plenty of examples of adaptation in the plant kingdom; before searching for more, it may be well to look at alternative explanations which may be just as interesting, and perhaps give us a slightly different view of the way in which evolution is working.

Acknowledgements

Thanks are due to Sue Antrobus, Rob Hammond, Tim Shreeve and Chris Sluman for their helpful comments and discussion.

References

- 1 Grubb, P.J. (1977) *Biol. Rev. Cambridge Philos. Soc.* 52, 107–145
- 2 van der Meijden, E. (1990) in *Toward a More Exact Ecology* (Grubb, P.J. and Whittaker, J.B., eds), pp. 163–181, Blackwell
- 3 Harper, J.L. (1977) *Population Biology of Plants*, Academic Press
- 4 Silvertown, J. (1987) *Introduction to Plant Population Ecology*, Longman
- 5 Lack, A.J. (1982) *New Phytol.* 91, 297–308
- 6 Primack, R.B. (1980) *J. Ecol.* 68, 849–862
- 7 Pors, B. and Werner, P.A. (1989) *Am. J. Bot.* 76, 1681–1688
- 8 Rathcke, B. and Lacey, E.P. (1985) *Annu. Rev. Ecol. Syst.* 16, 179–214
- 9 Primack, R.B. (1985) in *The Population Structure of Vegetation* (White, J., ed.), pp. 571–593, Dr W. Junk
- 10 Kochmer, J.P. and Handel, S.N. (1986) *Ecol. Monogr.* 56, 303–325
- 11 Primack, R.B. (1987) *Annu. Rev. Ecol. Syst.* 18, 409–430
- 12 Grime, J.P. and Mowforth, M.A. (1982) *Nature* 299, 151–153
- 13 Gross, R.S. and Werner, P.A. (1983) *Ecol. Monogr.* 53, 95–117
- 14 Feinsinger, P. (1978) *Ecol. Monogr.* 48, 268–287
- 15 Rabinowitz, D. et al. (1981) *Ecology* 62, 49–56
- 16 Waser, N.M. (1979) *Oecologia* 39, 107–121
- 17 Mooney, H.A. and Billings, W.D. (1961) *Ecol. Monogr.* 31, 1–29
- 18 Bullock, S.H., Beach, J.H. and Bawa, K. (1983) *Ecology* 62, 1494–1504
- 19 Dieringer, G. (1991) *Am. J. Bot.* 78, 497–503
- 20 Rathcke, B. (1988) *J. Ecol.* 78, 975–994
- 21 Lack, A.J. (1982) *New Phytol.* 91, 321–339
- 22 Rathcke, B.J. (1983) in *Pollination Biology* (Real, L., ed.), pp. 305–329, Academic Press
- 23 Feinsinger, P. (1987) *Trends Ecol. Evol.* 2, 123–126
- 24 Horvitz, C.C. and Schemske, D.W. (1990) *Ecology* 71, 1085–1097
- 25 Augspurger, C.K. (1981) *Ecology* 62, 775–788
- 26 Frankie, G.W. and Haber, W.A. (1983) in *Handbook of Experimental Pollination Biology* (Jones, C.E. and Little, R.J., eds), pp. 360–372, Van Nostrand Reinhold
- 27 Bawa, K.S. (1983) in *Handbook of Experimental Pollination Biology* (Jones, C.E. and Little, R.J., eds), pp. 394–410, Van Nostrand Reinhold
- 28 Zimmerman, M. (1980) *Ecology* 61, 502–506
- 29 Widén, B. (1991) *Oikos* 61, 205–215

TREE Subscriptions

All new subscriptions, renewals and subscription queries should be addressed to our Barking office at the address below.

- ☐ Personal subscriptions (1992, 12 monthly issues): £54.00 in the UK; \$83.00 in the USA and Canada; £59.00 elsewhere
- ☐ Library subscriptions (1992, 12 monthly issues plus hard-cover bound compendium with index): £239.00 in the UK and ROW
- ☐ Student subscriptions (1992, 12 monthly issues): £44.00 in the UK; \$68.00 in the USA and Canada; £49.00 elsewhere

(Student subscriptions must be accompanied by valid proof of student status.)

All prices include postage (air delivery outside UK). All subscriptions can be paid for by cheque, bank draft or UNESCO coupons. Personal and Library subscriptions can also be paid for by credit card – Access/Mastercard, Eurocard, Visa or American Express. Subscription orders should be sent to: Elsevier Science Publishers Ltd, Crown House, Linton Road, Barking, UK IG11 8JU. Tel. (outside UK): +44 81 5947272 Tel. (in UK): 081 594 7272