Seasonality of flowering and fruiting in temperate forest trees[1]

Martin J. Lechowicz

Abstract: The phenology of leaf presence and photosynthetic activity together set a potential limit on tree productivity in a seasonal climate; similarly, the seasonal timing of flowering and fruiting can decide tree reproductive success. The capacity for long-term storage of photosynthate appears to override any necessary functional linkage between these two critical aspects of tree phenology. Foliar and reproductive phenology in broadleaf deciduous trees of the temperate zone are only weakly coupled within a growing season, especially in precocious flowering trees that mature their fruits in early summer. In species that fruit in late summer and fall, leaf emergence and flowering can be entrained by shared responses to the progressive warming of early spring but with only limited effect on the timing of fruit maturation. The timing of foliar senescence and fruit maturation is correlated only in fall-fruiting trees but as a common response to fall climate rather than the outcome of foliar retranslocation of resources to developing fruits. The possibility exists that global climate change may disrupt these patterns of foliar and reproductive phenology, but the magnitude of the effect will depend on the poorly studied balance of thermal versus photoperiodic cues for phenological events.

Key words: phenology, leaf senescence, bud burst, seed dispersal, global climate change.

Résumé : La phénologie impliquant la présence simultanée des feuilles et de l'activité photosynthétique établit une limitation potentielle à la productivité des arbres sous un climat saisonnier; de la même manière, la chronologie saisonnière de la floraison et de la mise à fruit est déterminante pour le succès de la reproduction. La capacité d'accumuler des réserves à long terme sous forme de photosynthétats semble compenser tout lien fonctionnel nécessaire entre ces deux aspects critiques de la phénologie des arbres. Les phénologie foliaire et reproductive chez les espèces décidues à larges feuilles de la zone tempérée ne sont que faiblement couplées à l'intérieur d'une saison de croissance, surtout chez les arbres à floraison précoce dont les fruits mûrissent au début de l'été. Chez les espèces mûrissant à la fin de l'été ou à l'automne, l'émergence des feuilles et la floraison peuvent être déclenchées par des réactions reliées au réchauffement progressif au début du printemps, mais avec des effets limités sur la chronologie de la maturation des fruits. Le moment de la sénescense foliaire et de la maturation des fruits est corrélé seulement chez les arbres à fructification automnale, mais comme réaction commune au climat automnal plutôt que le début de la retranslocation foliaire des ressources vers le fruit en développement. Il est possible que le changement global du climat puisse perturber ces patrons de phénologie foliaire et reproductive, mais l'importance de l'effet dépend de la balance peu connue des déclencheurs photopériodiques versus les déclencheurs thermiques sur les événement phénologiques.

Mots clés : phénologie, sénescence foliaire, débourrement, dispersion des graines, changement global du climat.
[Traduit par la rédaction]

Introduction

Phenological observations have a long tradition, with substantial records beginning as early as the 16th century for temperate and boreal trees (Lieth 1974) augmented as well by many tropical observations since the 19th century (van Schaik et al. 1993). Observations of the date of particular phenophases (leaf emergence, flowering, fruiting, leaf senescence, and the like) for a species in a given locality are recorded, often in conjunction with weather records. Occasionally these observational records are collated and available in computerized databases (Polte-Rudolf 1993), but more often the data are scattered in relatively obscure government publications or local natural history journals. Some of the records are surprisingly long. For example, records of flowering dates for cherry (*Prunus* spp.) at Kyoto, Japan, date from the 8th century (Arakawa 1955). The Marsham phenology with annual records for the leafing and flowering of 10 woody species in southeastern England began in 1736

(Margary 1926; Kington 1974). Although ecologists have made some use of such long-term data records (Lieth 1974; Lechowicz 1984; Rathcke and Lacey 1985; Cannell 1990; Hänninen 1990; van Schaik et al. 1993), their full potential has not been exploited. These historical records are becoming increasingly important as we begin to investigate the ways that global change may alter the patterns of seasonality in northern regions (Cannell and Smith 1986; Kellomäki et al. 1988; Murray et al. 1989; Hänninen 1991, 1995).

Foliar phenology, which together with photosynthetic capacity sets the ultimate limit to gross primary production in a given region (Lieth 1974), has received the greatest attention. The dependence of leaf emergence on the gradual warming of late winter and early spring in temperate and boreal regions is understood reasonably well (Hunter and Lechowicz 1992; Hänninen 1990; Cannell 1990). The timing of flowering has also been related to thermal sums (Cannell 1989), as has the development of some fruits (Phillips 1922; Rathcke and Lacey 1985; Bellows et al. 1989). In general though, the ability to predict later season phenological events is poor. We can predict the timing of winter bud formation for conifers (Hänninen et al. 1990), but the timing of foliar senescence for deciduous trees and the timing of fruit maturation are less well understood. As global change alters the seasonality of temperature and rainfall in northern regions, the seasonal cues that govern tree phenology may well be altered fundamentally. Although the thermal regime in a locality may change, the seasonal photoperiodic cycle will not, and this could disrupt phenological events that respond to both temperature and photoperiod. Any changes in foliar phenology can influence photosynthetic productivity and therefore alter the amounts of photosynthate available for growth and reproduction. Changes in reproductive phenology potentially can change the reproductive success of trees in a region. Although we know that these foliar and reproductive functions are linked through storage of photosynthate (Kozlowski 1992), we do not know the degree to which their phenology is coordinated. The purpose of this brief review is to analyze long-term phenological records that provide a preliminary assessment of the coordination of foliar and reproductive phenology in broadleaf deciduous trees of the north temperate zone.

Materials and methods

I primarily analyze an historic record of tree phenology made by Thomas Mikesell between 1883 and 1912 in Wauseon, Ohio (Mikesell 1905; Smith 1915). This record includes the period of unusual weather associated with the eruption of Krakatoa (Hamilton 1986). Mikesell (1905) made daily observations of the weather and of phenological events of trees, first at his farm on the outskirts of Wauseon (Fulton County, Ohio: sec. 14, T7N, R6E; 41°36'N, 84°7'W, elevation 246 m) and after 1902 at his home in Wauseon (41°35'N, 84°7'W, elevation 240 m). The local landscape, which was first settled in the 1830s, is nearly level, with an elevational range of only about 10 m (Mikesell 1905). Wauseon was, and is, a small town surrounded by farmsteads cleared from native forest that typically retained some uncleared land as a woodlot; the nearby Goll Woods preserves a remnant of these native forests (Boerner and Cho 1987). Mikesell's (1905) observations probably included

trees planted in hedgerows as well as remnant patches of such native forest; certainly, the osage orange (*Maclura pomifera* (Rafinesque) Schneider) is native only in the Ozarks but was widely planted as a hedgerow tree in the Ohio territory during the 19th century (Barnes and Wagner 1981). We do not know how many trees of each species Mikesell observed, their consistency over the years, or their gender in the case of dioecious species. Mikesell does appear to have made all the observations himself, which would increase the consistency of observations from year to year. He was among the first weather observers in Ohio and was very conscientious and careful in his weather observations (Smith 1915); his phenological observations should not be any less so. Along with daily temperatures and precipitation, he recorded the dates of bud break, unfolding of leaves, completion of the full canopy, flowering, fruiting, first colouration of leaves, and full colour for 25 species of broadleaf deciduous trees. It is these historical records that form the basis for the following analyses and discussion, omitting only those species with too few reproductive data and *Hamamelis virginiana* L. because its peculiar phenological cycle spans two growing seasons.

The mean dates of leafing, flowering, and fruiting for each species are presented initially in relation to frost events that demarcate the growing season; the definitions of light and heavy frosts are based on Mikesell's recorded observations rather than any arbitrary air temperatures (Smith 1915). The years of record for reproductive events are not always the same, as all species did not flower or fruit every year, but these mean dates do provide a clear illustration of the basic patterns of seasonality in foliar and reproductive phenology in this temperate tree flora. The years with complete records for all foliar and reproductive events range from 4 to 15, with a median of 10 years.

A second analysis allows a more general comparison of the interrelationships between foliar and reproductive phenology among these diverse tree species. This analysis is based on the transformation of each phenological record to its deviation (in days) from the mean of that particular event and species. This essentially transforms all the species and events to a mean of zero and focuses attention on the patterns of deviation from the mean rather than on the mean itself in our comparisons among species and events. With graphs of these transformed data, we can readily consider, for example, whether late leafing is generally associated with late flowering. These transformed data thus provide a clear illustration of the general patterns of coordination between foliar and reproductive phenological events in this sample of broadleaf deciduous trees.

Finally, I also draw on a second phenological record taken between 1739 and 1925 that contains 134 years of leafing and flowering dates for hawthorn at the Marsham family estates near Norwich, England (Margary 1926; Kington 1974). I have excluded the years recorded from observations elsewhere. Unfortunately, the Marsham record does not specify the species of *Crataegus* observed, and there are at least two likely candidates in this region: the hawthorn *C. monogyna* Jacq. and the Midland hawthorn *C. laevigata* (Poiret) DC. (Stace 1991). It is possible but not too likely that the record confounds the two species, and more likely the earlier of the two species was observed consistently (Margary 1926). Stillingfleet (1791) lived at the Marsham estate in 1755 and

Fig. 1. Mean dates of flowering and leafing for 23 broadleaf deciduous tree species growing near Wauseon, Ohio, between 1893 and 1912 together with the mean dates of frost events observed at the site (data from Smith 1915). Ag, *Aesculus glabra* Willdenow; Am, *Acer saccharum* Marshall; An, *Acer negundo* L.; Asm, *Acer saccharinum* L.; Cf, *Cornus florida* L.; Cg, *Carya glabra* (Miller) Sweet; Co, *Carya ovata* (Miller) K. Koch; Dv, *Diospyros virginiana* L.; Fa, *Fraxinus americana* L.; Fn, *Fraxinus nigra* Marshall; Jn, *Juglans nigra* L.; Mp, *Maclura pomifera* (Rafinesque) Schneider; Ov, *Ostrya virginiana* (Miller) K. Koch; Pd, *Populus deltoides* Marshall; Pt, *Populus tremuloides* Michaux; Po, *Platanus occidentalis* L.; Qa, *Quercus alba* L.; Qb, *Quercus bicolor* Willdenow; Qm, *Quercus macrocarpa* Michaux; Qv, *Quercus velutina* Lamarck; Rt, *Rhus typhina* L.; Sa, *Sassafras albidum* (Nuttall) Nees; Sn, *Salix nigra* Marshall; Ua, *Ulmus americana* L.


Mean Julian day of flowering
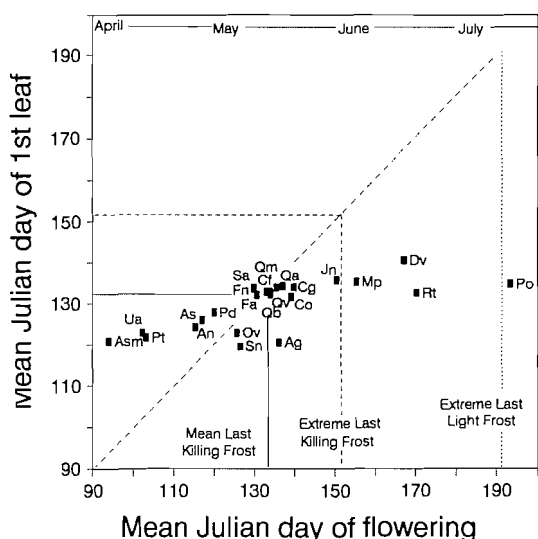
also recorded phenological observations; his record specifies observing the white hawthorn *Crataegus oxyacantha*, which today would be *C. laevigata*. Unlike Mikesell, the Marsham family did not record weather data and I have resorted to the use of a generalized record for central England (Manley 1974) to compare the long-term trends between spring temperatures and the dates of flowering and leafing.

Results and discussion

Two critical functions coincide in mature trees, namely photosynthetic production and reproduction. The phenomenon of mast fruiting or alternate bearing, in which trees produce significant seed crops only at intervals rather than annually, is common in trees (Silvertown 1980; Monselise and Goldschmidt 1982) and suggests that these two functions compete to at least some degree for a common resource pool. Mast fruiting also suggests that trees can sequester reserves of photosynthate and mineral nutrients, and diverse data support the role of such storage in tree growth and reproduction (Kozlowski 1992). Given the frequent coordination of reproductive and productive functions across years, we might expect related coordination within an annual cycle. For example, if developing fruits depend on either current photosynthate or retranslocation of mineral nutrients from

Fig. 2. Mean dates of flowering and fruiting for 23 broadleaf deciduous tree species growing near Wauseon, Ohio, between 1893 and 1912 together with the mean dates of frost events observed at the site. The database, species, and their abbreviations are as in Fig. 1.
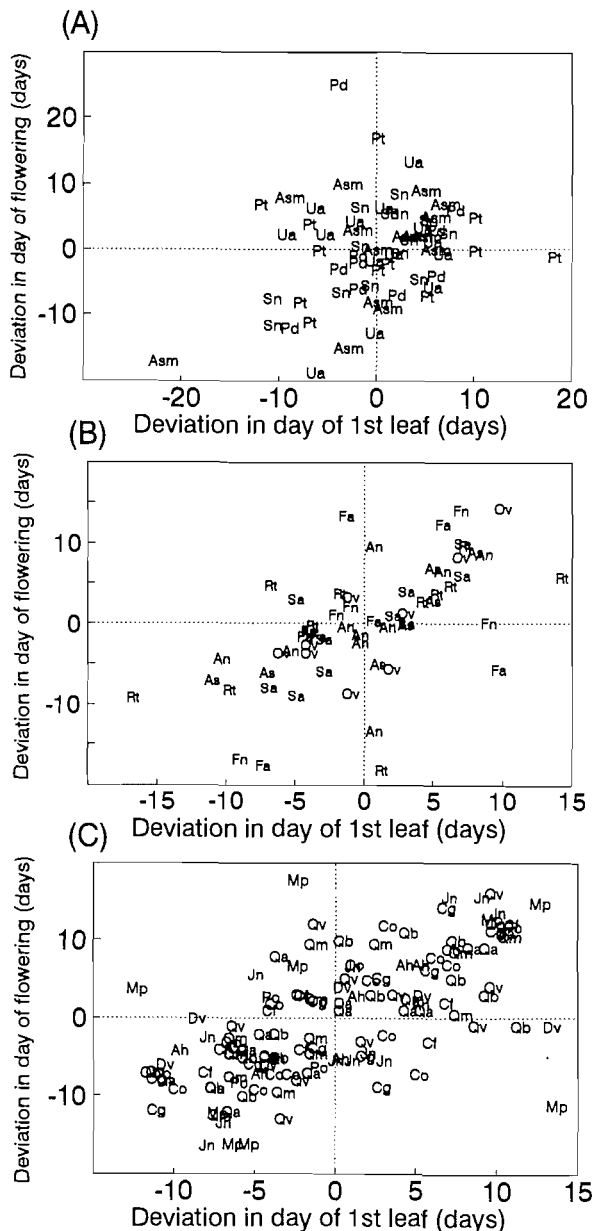

Mean Julian day of flowering
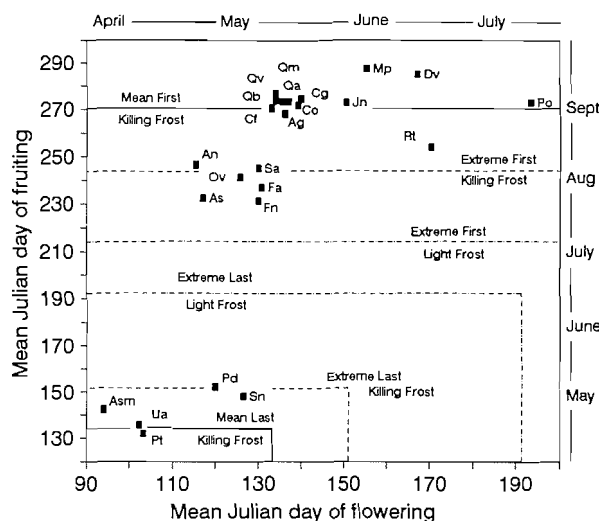
foliage, then we might expect a consistent relationship between the timing of foliar senescence and fruit maturation. Such intraannual coordination will be expressed in patterns in the long-term records of phenology governing production (foliar emergence and senescence) and reproduction (flowering and fruiting). Thus long-term records of foliar and reproductive phenology provide an opportunity to test for the occurrence of coordinated responses in the timing of phenological events within an annual cycle.

Seasonality of leafing, flowering, and fruiting

Most of these Ohio trees leaf out within a fairly narrow time period in spring but flower and fruit over a much more extended period. During a typical growing season, one tree species or another is forming its first leaves during a span of about 23 days, whereas flowering is occurring during about 78 days and fruiting during about 156 days on average from analysis of data in Smith (1915). The modal group of species leafs out and flowers more or less simultaneously and in conjunction with the mean date of the last killing frost in spring (Fig. 1). This includes ashes (*Fraxinus*), hickories (*Carya*), sassafras (*Sassafras*), and oaks (*Quercus*) with ring-porous wood anatomy as well as the diffuse-porous dogwood (*Cornus*). With the exception of elm (*Ulmus*), which has peculiar wood anatomy (Lechowicz 1984), the species that typically leaf out and flower in advance of the last killing frost are diffuse-porous maples (*Acer*) and poplars (*Populus*). These patterns of foliar phenology are consistent with the expectation that ring-porous species can only leaf out after vascular tissue rendered nonfunctional over winter has been replaced by cambial activity (Lechowicz 1984; Wang et al. 1992); flowering phenology follows a similar pattern. Willow (*Salix*), ironwood (*Ostrya*), and Ohio buckeye (*Aesculus*) leaf out in advance of the last killing frost and flower soon thereafter. Walnut (*Juglans*) leafs out just after the average occurrence of the last killing frost and flowers just as the last danger of killing frost fades. Osage orange
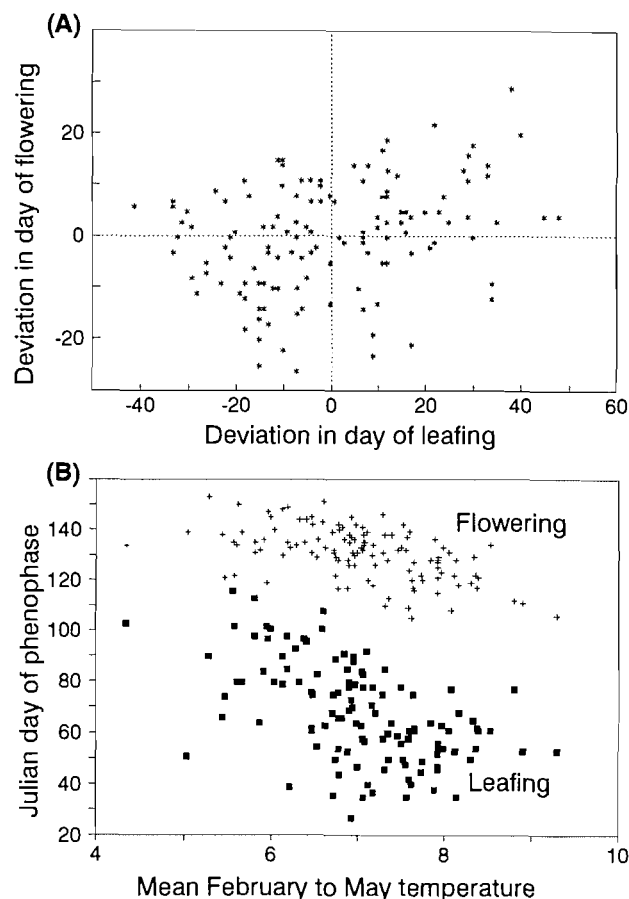
Fig. 3. Relationship between the normalized deviations from a mean of zero in flowering and leafing for broadleaf deciduous trees that mature their fruits in (A) early summer (Spearman's $\tau = 0.241$, $p = 0.051$), (B) late summer ($\tau = 0.672$, $p = 0.0001$), and (C) fall ($\tau = 0.658$, $p = 0.0001$). The database, species, and their abbreviations are as in Fig. 1.

Fig. 4. (A) Relationship between the normalized deviations from a mean of zero in flowering and leafing for *Crataegus* in southeastern England (Margary 1926; Kington 1974). Spearman's $\tau = 0.344$ and $p = 0.0001$ for this relationship. (B) Relationships between these phenological events and the temperatures during the later winter and spring (weather data from Manley 1974).

(*Maclura*), persimmon (*Diospyros*), sumac (*Rhus*), and sycamore (*Platanus*) leaf out just before or after the danger of killing frost is completely past, and flower much later. Sycamore, the only diffuse-porous species among these four, flowers extremely late in the season when there is no danger of even light frost.

The timing of fruit maturation in these Ohio broadleaf trees falls in three fairly distinct groups, which are only partly related to their foliar phenology (Fig. 2). There is a group of precocious flowering species that mature and disperse their fruits early in the season, more or less coincident with the end of danger of killing frosts. These early summer

fruiting species include willow, elm, one maple, and the poplars. These are species with seed that germinate immediately and depend on wet depressions or river-shore habitats created by spring floods for seedling establishment (Burns and Honkala 1990). Other species of maple, ironwood, sassafras, and ash that flower in the same period in early spring take much longer to mature and disperse their fruits. These late summer fruiting species disperse seed just before the danger of killing frost returns in the fall, but they primarily have dormant seed that only germinate after winter (Schopmeyer 1974; Burns and Honkala 1990). The remaining species are fall fruiting and typically disperse their fruit only after killing frosts occur. These include the nut-bearing oaks, hickories, and walnuts as well as the sumac, osage orange, persimmon, and sycamore, all of which also require cold hardening to germinate (Schopmeyer 1974; Burns and Honkala 1990).

Interrelationships in the timing of leafing, flowering, and fruiting

Later leafing in a given year is associated with later flowering, although this trend is fairly weak in trees that fruit in early summer (Fig. 3). The rank order comparison of the

Fig. 5. Relationship between the normalized deviations from a mean of zero in dates of flowering and fruiting for broadleaf deciduous trees that mature their fruits in (A) early summer ($\tau = 0.300$, $p = 0.014$), (B) late summer ($\tau = 0.432$, $p = 0.002$), and (C) fall ($\tau = 0.200$, $p = 0.016$). The database, species, and their abbreviations are as in Fig. 1.
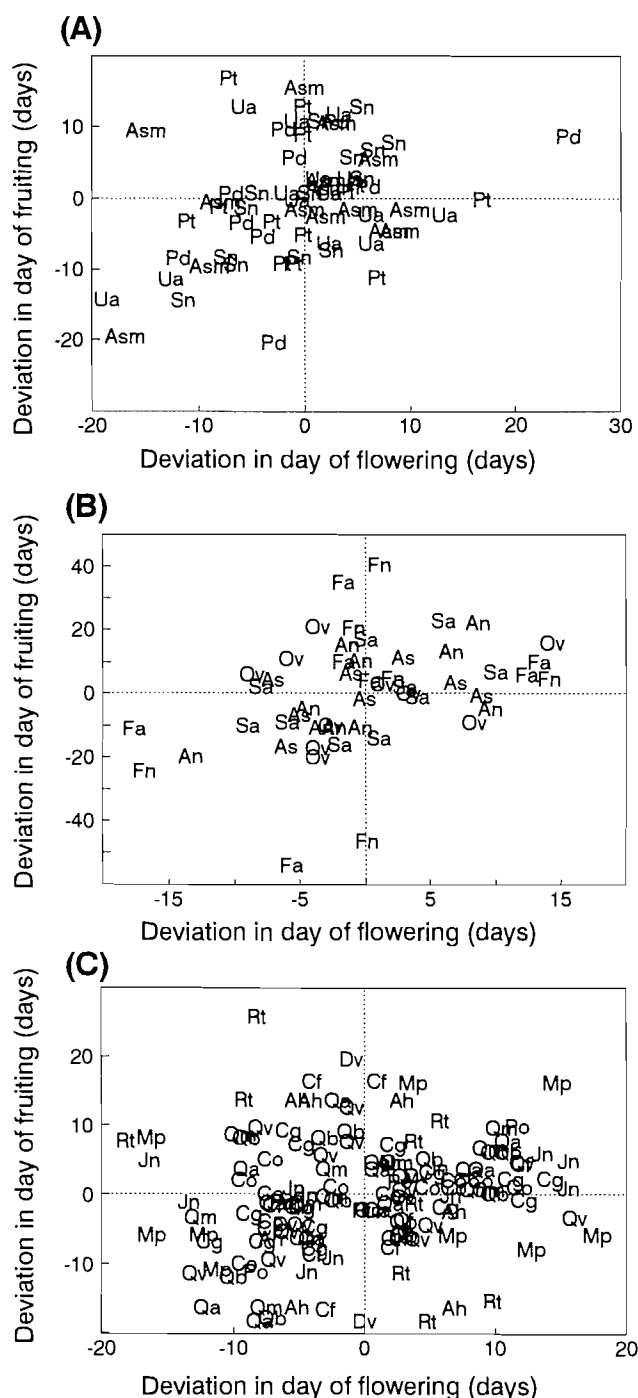
are fewer than one would expect by chance alone. This association might arise from (*i*) a sequential dependency in the two functions (Borchert 1992), (*ii*) the shared dependency on an external variable like cumulative temperature (Hunter and Lechowicz 1992), or (*iii*) a combination of the endogenous functional organization and responses to a common exogenous variable. We do not have the data to evaluate these possible causal mechanisms for a linkage between foliar and flowering phenology.

The much longer Marsham record for *Crataegus* validates the trends apparent in the relatively short Mikesell record (Fig. 4). The same positive association between leafing and flowering times is apparent (Fig. 4A), and additionally the timing of both events is similarly correlated with late winter and spring temperatures (Fig. 4B). There is, however, less scatter in the relationship between flowering time and temperature, which suggests some functional independence of the two events.

If flowering is delayed when leaves emerge late, we might expect fruit maturation to also be delayed. This indeed is the case in Ohio regardless of the seasonal timing of fruit maturation, but the relationships are weak (Fig. 5). The effects of a late spring do tend to carry over and retard fruit development to some degree. In early summer fruiting trees, leafing, flowering, and fruiting are all subject to essentially the same weather conditions; a cool spring can account for delays in all three phenophases. This explanation, however, is not likely to explain delays in late summer and fall fruiting. In eastern North America, late and cold springs do not necessarily lead to cool summers or an early fall (Bell et al. 1993). In these later fruiting trees, such retarded fruit maturation may be due to some endogenous regulation of the sequence of resource partitioning. For example, perhaps fruit maturation cannot proceed quickly while stored reserves of photosynthate are being replenished (cf. Kozlowski 1992).

A similar trade-off could also govern the timing of fruit maturation versus foliar senescence. If developing fruits draw on resources needed for leaf maintenance or on resources translocated from leaves, then such trade-offs in partitioning occur; we might expect that late fruiting would also be associated with later leaf senescence. This is only the case in fall-fruiting trees (Fig. 6), and then it seems to arise more from the opportunity to take advantage of a late fall to continue both photosynthetic activity and fruit maturation. The negative correlation that would indicate translocation of resources from foliage to developing fruits is absent. Stored resources appear to functionally uncouple the maturation of fruits and foliar phenology, indicating the possible generality of such uncoupling in well-studied trees like pecan and apple (Kozlowski 1992).

Directions for future research on the responses of tree reproductive phenology to global change

How might the coordination of foliar and reproductive phenology in north temperate trees be disrupted by global change? For example, what would happen if the growing season were somewhat longer and warmer, perhaps more subject to early or late frosts or to occasional drought, but on the whole not so dramatically different in its seasonal structure as has been predicted (Manabe et al. 1992)? On the one hand, the strong codependence on temperature then suggests

leafing and flowering deviates is significant. Additionally, in all cases there is a preponderance of joint events in the + + and − − quadrants; that is, if leafing is early (or late) in a given year, then so is flowering likely to be. Years in which + − combinations of flowering and leafing deviations occur

Fig. 6. Relationship between the normalized deviations from a mean of zero in dates of fruiting and foliar senescence for broadleaf deciduous trees that mature their fruits in (A) early summer ($r = 0.080$, $p = 0.521$), (B) late summer ($r = 0.091$, $p = 0.524$), and (C) fall ($r = 0.199$, $p = 0.017$). The database, species, and their abbreviations are as in Fig. 1.
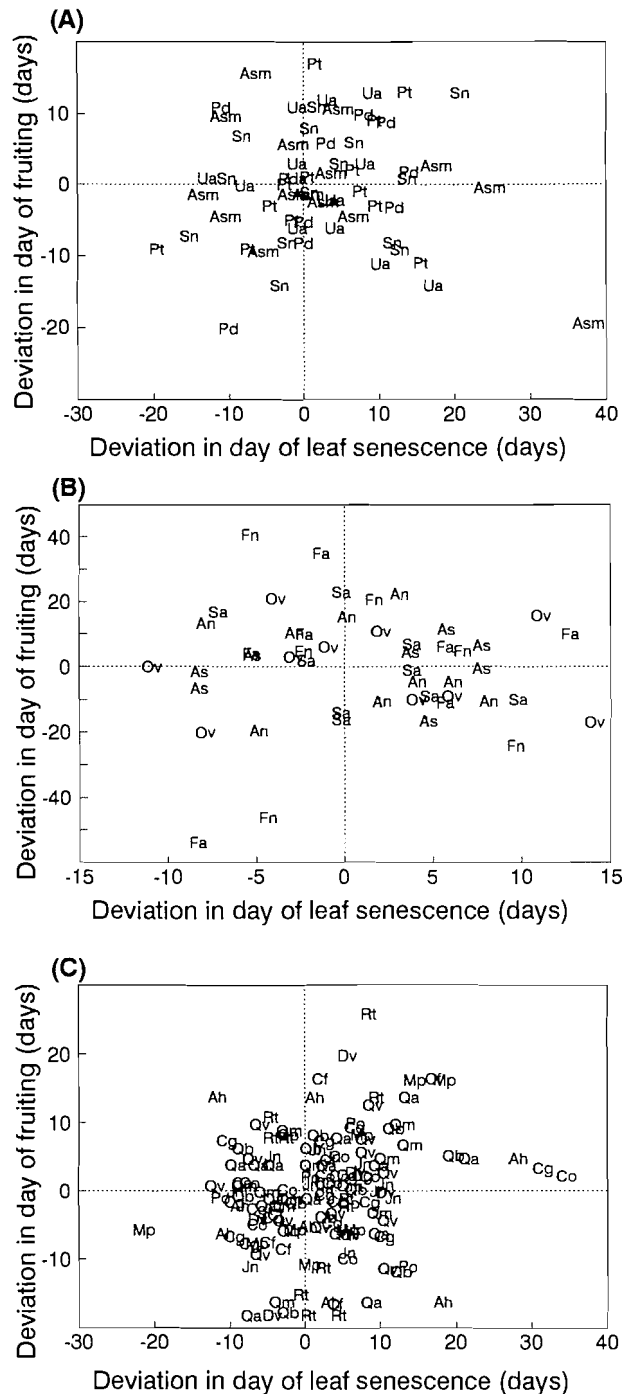
Fig. 7. An example of the diversity of reproductive phenology in the tropics from monthly records of flowering and fruiting by 190 tree species in Guyana between 1881 and 1989 (Steege and Persaud 1991). Species from families with temperate members (+) do not show any distinctly different pattern of reproductive seasonality than species from strictly tropical families (*).
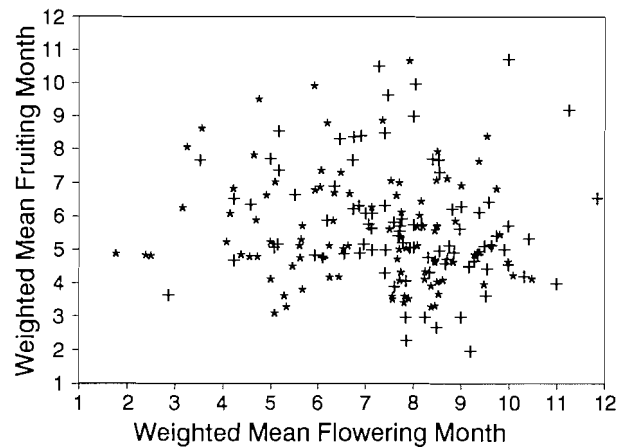
other hand, photoperiodic stimuli also contribute to the foliar and reproductive phenology in at least some tree species (Powell et al. 1986; Hunter and Lechowicz 1992; Heide 1993). This could lead to disruption of phenological patterns as the climatic regimes at a locality change but of necessity the annual photoperiodic cycle is unaltered (Hänninen 1991; Heide 1993). To predict the potential impacts of climate change on tree phenology we must investigate more thoroughly the balance of thermal and photoperiodic cues for phenological events.

To understand the nature of phenological coordination we will also have to turn to comparative studies of tropical as well as other temperate species. The tropical and temperate floras have long histories of independent evolution (Vakhrameev 1991; Behrensmeyer et al. 1992), but the temperate flora did exist in a more tropical, seasonal climate during the Early to Middle Eocene (Janis 1993). These northern paleotropics, however, were subject to an annual photoperiodic cycle of much greater range than the present tropics. The degree to which present phenological patterns reflect evolutionary opportunities and constraints arising in these distinct thermic and photoperiodic regimes is an open question that can best be answered through more extensive comparisons of tropical and temperate trees. Even today tropical regions have seasonality and the phenology of tropical trees responds to seasonal patterns of both abiotic and biotic resources (van Schaik et al. 1993; Borchert 1992, 1994). In Guyana forests, for example, flowering peaks in the long dry season of fall, and fruiting in the short dry season of spring (Steege and Persaud 1991), but both phenological events can occur in virtually any month for one species or another. There is no immediate indication that present tropical trees are constrained to flower in only a particular season, nor that families with temperate members are restricted within narrower seasonal limits (Fig. 7). Phenology is only a part of the functional organization of trees and is linked to other

that phenological coordination will be adjusted readily as the climate changes. Certainly the coordination has not been impaired by interannual variation that probably exceeds what may occur due to the changing climate at a locality. On the

aspects of tree form and function (Lechowicz 1984; Wang et al. 1992). The rich opportunities for the comparative investigation of tree phenology in the tropical and temperate floras should be exploited.

Acknowledgements

References

Arakawa, H. 1955. Twelve centuries of blooming dates of the cherry blossoms at the city of Kyoto and its own vicinity. Pure Appl. Geophys. **30**: 147–150.

Barnes, B.V., and Wagner, W.H., Jr. 1981. Michigan trees. A guide to the trees of Michigan and the Great Lakes region. University of Michigan Press, Ann Arbor, Mich.

Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D., and Wing, S.L. 1992. Terrestrial ecosystems through time. Evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago, Ill.

Bell, G., Lechowicz, M.J., Appenzeller, A., Chandler, M., DeBlois, E., Jackson, L., Mackenzie, B., Preziosi, R., Schallenberg, M., and Tinker, N. 1993. The spatial structure of the physical environment. Oecologia, **96**: 114–121.

Bellows, T.S., Jr., Morse, J.G., and Lovatt, C.J. 1989. Modelling flower development in citrus. *In* Manipulation of fruiting. *Edited by* C.J. Wright. Butterworth and Co. (Publishers) Ltd., London. pp. 115–129.

Boerner, R.E.J., and Cho, D. 1987. Structure and composition of Goll Woods, an old-growth forest remnant in northwestern Ohio. Bull. Torrey Bot. Club, **114**: 173–179.

Borchert, R. 1992. Computer simulation of tree growth periodicity and climatic hydroperiodicity in tropical forests. Biotropica, **24**: 385–395.

Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology, **75**: 1437–1449.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Vol. 2. Hardwoods. USDA Forest Service, Washington, D.C.

Cannell, M.G.R. 1989. Chilling, thermal time and the date of flowering of trees. *In* Manipulation of fruiting. *Edited by* C.J. Wright. Butterworth and Co. (Publishers) Ltd., London. pp. 99–113.

Cannell, M.G.R. 1990. Modelling the phenology of trees. *In* Modelling to understand forest functions. Silva Carelica 15. *Edited by* H. Jozefek. University of Joensuu, Joensuu, Finland. pp. 11–27.

Cannell, M.G.R., and Smith, R.I. 1986. Climatic warming, spring budburst and frost damage on trees. J. Appl. Ecol. **23**: 177–191.

Hamilton, K. 1986. Early Canadian weather observers and the "year without a summer." Bull. Am. Meteorol. Soc. **67**: 524–532.

Hänninen, H. 1990. Modelling bud dormancy release in trees from cool and temperate regions. Acta For. Fenn. **213**: 1–47.

Hänninen, H. 1991. Does climatic warming increase the risk of frost damage in northern trees? Plant Cell Environ. **14**: 449–454.

Hänninen, H. 1994. Effects of climatic change on trees from the cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. Can. J. Bot. **73**: 000–000.

Hänninen, H., Hakkinen, R., Hari, P., and Koski, V. 1990. Timing of growth cessation in relation to climatic adaptation of northern woody plants. Tree Physiol. **6**: 29–39.

Heide, O.M. 1993. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. Physiol. Plant. **88**: 531–540.

Hunter, A.F., and Lechowicz, M.J. 1992. Predicting the timing of budburst in temperate trees. J. Appl. Ecol. **29**: 597–604.

Janis, C.M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. Annu. Rev. Ecol. Syst. **24**: 467–500.

Kellomäki, S., Hänninen, H., and Kolstrom, T. 1988. Model computations on the impacts of the climatic change on the productivity and silvicultural management of the forest ecosystem. Silva Fenn. **22**: 293–305.

Kington, J.A. 1974. An application of phenological data to historical climatology. Weather, **29**: 320–328.

Kozlowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. Bot. Rev. **58**: 107–222.

Lechowicz, M.J. 1984. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. Am. Nat. **124**: 821–842.

Lieth, H. (*Editor.*) 1974. Phenology and seasonality modelling. Springer Verlag, New York.

Manabe, S., Spelman, M.J., and Stouffer, R.J. 1992. Transient responses of a coupled ocean–atmosphere model to gradual changes of atmospheric CO_2. Part II. Seasonal response. J. Climatol. **5**: 105–126.

Manley, G. 1974. Central England temperatures: monthly means 1659 to 1973. Q. J. R. Meteorol. Soc. **100**: 389–405.

Margary, I.D. 1926. The Marsham phenological record in Norfolk, 1736–1925, and some others. Q. J. R. Meteorol. Soc. **51**: 27–54.

Mikesell, T. 1905. The county of Fulton: a history of Fulton County, Ohio from the earliest days. Northwestern Historical Association, Madison, Wis.

Monselise, S.P., and Goldschmidt, E.E. 1982. Alternate bearing in fruit trees. Hortic. Rev. **4**: 128−173.

Murray, M.B., Cannell, M.G.R., and Smith, R.I. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. J. Appl. Ecol. **26**: 693−700.

Phillips, H.A. 1922. Effect of climatic conditions on the blooming and ripening dates of fruit trees. N.Y. Agric. Exp. Stn. (Ithaca) Mem. 59. pp. 1383−1416.

Polte-Rudolf, C. 1993. The IPG data bank at the Deutscher Wetterdienst. Arbor. Phaenol. **38**: 28−31.

Powell, L.E, Swartz, H.J., Pasternak, G., and Maybee, C.G. 1986. Time of flowering in spring: its regulation in temperate zone woody plants. Biol. Plant. **28**: 81−84.

Rathcke, B., and Lacey, E.P. 1985. Phenological patterns of terrestrial plants. Annu. Rev. Ecol. Syst. **16**: 179−214.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. USDA Forest Service, Washington, D.C.

Silvertown, J.W. 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linn. Soc. **14**: 235−250.

Smith, J.W. 1915. Phenological dates and meteorological data recorded by Thomas Mikesell at Wauseon, Fulton County, Ohio. Mon. Weather Rev. Suppl. **2**: 21−93.

Stace, C. 1991. New flora of the British Isles. Cambridge University Press, Cambridge, England.

Steege, H. ter, and Persaud, C.A. 1991. The phenology of Guyanese timber species: a compilation of a century of observations. Vegetatio, **95**: 177−198.

Stillingfleet, B. 1791. The calendar of flora, Swedish and English. *In* Miscellaneous tracts relating to natural history, husbandry, and physick. J. Dodsley, London. pp. 223−337.

Vakhrameev, V.A. 1991. Jurassic and Cretaceous floras and climates of the Earth. Cambridge University Press, Cambridge, England.

van Schaik, C.P., Terborgh, J.W., and Wright, S.J. 1993. The phenology of tropical forests: Adaptive significance and consequences for the primary consumers. Annu. Rev. Ecol. Syst. **24**: 353−377.

Wang, J., Ives, N.E., and Lechowicz, M.J. 1992. The relation of foliar phenology to xylem embolism in trees. Funct. Ecol. **6**: 469−475.