*Annals of Botany* **100**: 1271–1285, 2007
doi:10.1093/aob/mcm206, available online at www.aob.oxfordjournals.org

OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

# Synchronous Pulsed Flowering: Analysis of the Flowering Phenology in *Juncus* (Juncaceae)

STEFAN G. MICHALSKI* and WALTER DURKA

*Helmholtz Centre for Environmental Research – UFZ, Department of Community Ecology (BZF), Theodor-Lieser-Strasse 4, D-06120 Halle, Germany*

Received: 16 May 2007 Returned for revision: 29 June 2007 Accepted: 16 July 2007 Published electronically: 19 September 2007

• *Background and Aims* The timing of flowering within and among individuals is of fundamental biological importance because of its influence on total seed production and, ultimately, fitness. Traditional descriptive parameters of flowering phenology focus on onset and duration of flowering and on synchrony among individuals. These parameters do not adequately account for variability in flowering across the flowering duration at individual and population level. This study aims to analyse the flowering phenology of wind-pollinated *Juncus* species that has been described as temporally highly variable ('pulsed flowering'). Additionally, an attempt is made to identify proximate environmental factors that may cue the flowering, and ultimate causes for the flowering patterns are discussed.
• *Methods* Flowering phenology was examined in populations of nine *Juncus* species by estimating flowering synchrony and by using the coefficient of variation (CV) to describe the temporal variation in flowering on individual and population levels. Phenologies were compared with null models to test which patterns deviate from random flowering. All parameters assessed were compared with each other and the performance of the parameters in response to randomization and varying synchrony was evaluated using a model population. Flowering patterns were correlated with temperature and humidity.
• *Key Results* Most flowering patterns of *Juncus* were best described as synchronous pulsed flowering, characterized as population-wide concerted flowering events separated by days with no or few open flowers. Flowering synchrony and variability differed from a random pattern in most cases. CV values in combination with a measure of synchrony differentiated among flowering patterns found. Synchrony varied among species and was independent from variability in flowering. Neither temperature nor humidity could be determined as potential cues for the flowering pulses.
• *Conclusions* The results indicate that selection may act independently on synchrony and variability. We propose that synchronous pulsed flowering in *Juncus* is an evolved strategy that provides selective benefits by increasing outcrossing and by spreading the risk of reproductive failure.

**Key words:** *Juncus*, flowering phenology, synchrony, pollination efficiency, wind pollination.

## INTRODUCTION

Flowering phenology is an important life history trait because the timing of reproduction and the schedule of reproductive expenditures across time can strongly influence individual fitness (Primack, 1985; Rathke and Lacey, 1985; Fenner, 1998). Similar to other phenological events that can occur more or less simultaneously within and among plant populations such as germination or leafing, the proximate and ultimate factors that determine the evolution and maintenance of flowering phenologies are of fundamental interest for the understanding of species interaction and community functions (Fenner, 1998).

Flowering phenology has been mainly analysed with respect to flowering onset and duration of flowering. Gentry (1974) described generally accepted syndromes as the so-called 'mass flowering', with short flowering durations and masses of flowers produced, or the 'steady-state flowering' with extended flowering durations and only a few flowers produced per day, and variations in between these extremes. Most temperate plants show the 'cornucopia' type of flowering in which a substantial number of flowers is displayed over several weeks (Gentry, 1974). A quantitative characterization of the flowering phenology is possible by examining the flowering distribution curve, i.e. the number of open flowers per census for the whole flowering duration (Rathke and Lacey, 1985). In many species flowering begins with a maximum and then tails off leading to positively skewed distributions (Thomson, 1980; but see, for example, Silberbauer-Gottsberger, 2001). For unimodal flowering phenologies, characteristics such as duration, skewness or kurtosis of flowering can be parameterized, allowing the comparison between species (Malo, 2002). The temporal distribution of an individual's flowering in relation to that of other population members leads to measures of overlap in flowering time or synchrony (Primack, 1980; 1985). Apart from onset, duration, kurtosis and skewness of flowering a number of parameters measuring flowering synchrony have been developed (see below; Primack, 1980; Augspurger, 1983; Marquis, 1988; Murali and Sukumar, 1994; Bolmgren, 1998; Albert *et al.*, 2001; Mahoro, 2002; Fenner *et al.*, 2002).

Information about the timing of onset, the duration and synchrony of flowering may be satisfactory to describe the most common case of flowering phenologies: the unimodal temporal distribution in which flowers are continually produced with a more or less pronounced maximum. However, the opening of flowers may not show unimodal distributions (Eriksson, 1995; Pico and Retana, 2000) or

* For correspondence. E-mail Stefan.Michalski@ufz.de

may vary within and among individuals during their flowering time as, for example, the temporal clustering within umbels of *Butomus umbellatus* (Bhardwaj and Eckert, 2001). Synchrony in such flowering patterns within and among individuals will lead to pulses of flowering at individual and population level. Traditionally used parameters like flowering duration and synchrony do not adequately describe such flowering phenologies.

The coefficient of variation (CV) defined as the standard deviation relative to the mean number of open flowers per day could provide a measure of temporal variation in flowering. The coefficient of variation at population level ($CV_p$) has been used widely in mast seeding/mast flowering research to estimate the degree of annual variation in seed output within a population (Silvertown, 1980; Kelly, 1994). A high $CV_p$ can be the result of a highly variable and unsynchronized behaviour of the individuals or of a moderate individual variation combined with a high among-individual synchrony. Hence, identical $CV_p$ values may reflect different biological causes. Therefore it was proposed to dissect the $CV_p$ into within-individual variability and among-individual synchrony to allow for the determination of their relative contributions (Herrera, 1998).

Since the early works of Sprengel (1793) and Knuth (1898) flower biology was interpreted as being driven by ecological and evolutionary causes. In particular, the timing of reproduction and the schedule of flowering are strongly influenced by various proximate and ultimate causes (Rathke and Lacey, 1985; Fenner, 1998). Flowering as a physiological stage and a critical event in the life cycle is not independent of other phenophases. Resource status and the vegetative development of a plant can constrain its flowering pattern (Ollerton and Lack, 1998; Sola and Ehrlen, 2007). On the other hand, flowering precedes the development of seeds that again can be limited by the availability of resources.

Environmental cues like temperature, humidity or irradiance are known to influence different aspects of flowering phenology. For example, synchronous flowering or seed set may be associated with seasonal changes in irradiance (e.g. Adler and Kielpinski, 2000) or temperature (e.g. Schauber *et al.*, 2002). In many tropical species rainfall is a triggering mechanism for flowering and thus an important factor for ensuring synchronization of flowering within populations (Opler *et al.*, 1976). Furthermore, Proença and Gibbs (1994) proposed air humidity as an environmental factor responsible for the induction of flowering in tropical species with a 'big-bang' flowering strategy. Temperature affects the rates of flower development and thus can lead to variation of flowering within a flowering season (Bertin and Sholes, 1993; Murza and Davis, 2005). Also, the onset of flowering in temperate perennial herbs can be related to the accumulation of heat sums above a certain threshold (Rathke and Lacey, 1985; e.g. Diekmann, 1996). Pollination in anemophilous species should be restricted to dry conditions (Regal, 1982; Ackerman, 2000; Culley *et al.*, 2002). For instance, although temperature in *Ambrosia artemisiifolia* controls anther extension, pollen sac dehiscence is governed by relative humidity (Bianchi *et al.*, 1959). A number of studies found similar relationships between humidity and anther dehiscence and thus pollen release in wind-pollinated species (e.g. Lisci *et al.*, 1994; Bianchini and Pacini, 1996; Sharma *et al.*, 1998; Matsui *et al.*, 1999).

A variety of selective factors may act as ultimate causes for the timing of flowering on both population and individual levels. Population flowering phenology is the sum of the flowering behaviour of the individuals. Hence, the main aspects on which potential selection on the schedule of flowering could act are the flowering duration of the individual, the distribution of open flowers within the individuals' flowering duration and the interaction among individuals by means of among-individual synchrony of flowering. For example, synchronous flowering may attract pollinators due to increased floral display and should promote outcrossing by maximizing the number of potential mates. In fact, high flowering synchrony has been shown to increase reproductive output (Augspurger, 1981; Marquis, 1988; Mahoro, 2002; but see Primack, 1980; McIntosh, 2002; Buide *et al.*, 2002). However, slight asynchrony has also been described as beneficial for individual fitness if it forces pollinators to move between individuals (Rathke and Lacey, 1985). Flowering patterns may also be an adaptation to the influence of herbivores or seed predators (Janzen, 1976; Augspurger, 1981).

Despite the widespread occurrence of anemophily, wind pollination has been studied far less than zoophilous pollination systems (Ackerman, 2000; Harder, 2000; Barrett, 2002; Culley *et al.*, 2002). Because pollination by wind is mostly an undirected process driven largely by abiotic factors, anemophilous pollen transfer is often considered as inefficient (e.g. Whitehead, 1969; Faegri and van der Pijl, 1979). Certain floral characters have been found typically associated with wind-pollination and may facilitate this process. The anemophilous pollination syndrome is often characterized by a reduced or absent perianth, exposed stigmata with an enlarged surface, a reduced number of ovules and, in particular, by high pollen production (Pohl, 1929; Faegri and van der Pijl, 1979; Ackerman, 2000; Culley *et al.*, 2002). The release of pollen in wind-pollinated trees should be advantageous early in the growing season before canopy closure thus reducing the interference of pollen transport with the foliage (Whitehead, 1969; Heinrich, 1976; Faegri and van der Pijl, 1979; Bolmgren *et al.*, 2003). However, for herbaceous species, onset of flowering has been found less determined (Bolmgren *et al.*, 2003). Because of the passive nature of anemophily it has been stated that wind-pollinated plants release large quantities of pollen following specific environmental cues (Bianchi *et al.*, 1959; Faegri and van der Pijl, 1979; Whitehead, 1983; Cox, 1991; Culley *et al.*, 2002). The efficiency of pollination in wind-pollinated plants may be enhanced by high flower densities, intrapopulation synchronization and shorter durations of flowering (Whitehead, 1969; Melampy and Hayworth, 1980; Rabinowitz *et al.*, 1981; Allison, 1990).

Flowering phenology and reproductive biology in the wind-pollinated genus *Juncus* was last studied intensely more than a century ago (Buchenau, 1890, 1892). Buchenau reported the occurrence of what he called 'flowering in pulses' in many *Juncus* species. He observed that flowering

of some species at a locality is highly variable over time but synchronized among individuals. Flowers of *Juncus* are hermaphroditic and slightly protogynous. An individual chasmogamous *Juncus* flower opens only once for a few hours and very rarely for longer than 24 h. In many *Juncus* species all individuals of a population open their flowers synchronously on a given day followed by days without any open flowers. However, Buchenau could not determine any environmental cues for the flowering pulses.

In this study, the flowering phenology in populations of nine *Juncus* species is documented and pulsed flowering identified as a typical pattern. A comprehensive set of descriptive parameters is used that is necessary to analyse the different aspects of flowering phenologies on which selection may act is used. Null models are used to test whether the degrees of variability or synchrony deviate from patterns expected by chance. The performance of the parameters in response to randomization and varying synchrony is investigated in a model population. Selection may act independently on different aspects of phenologies, e.g. on within-individual variability or among-individual synchrony as has been proposed for masting phenologies (Koenig *et al.*, 2003). This hypothesis is tested on flowering phenologies by comparing *Juncus* species with each other and with other taxa in respect to the degree of synchrony and temporal variability of flowering and the relationships among the parameters studied. In general, flowering in wind-pollinated species should be co-ordinated by unambiguous environmental cues (Whitehead, 1983). For *J. compressus*, flowering pulses have been described as favoured by warmer temperatures and high humidity (Graebner, 1934). Hence, these environmental variables are investigated as potential cues for the flowering patterns in the *Juncus* species studied. Finally the potential adaptive value of synchronous pulsed flowering is discussed.

## MATERIALS AND METHODS

### *Species and study site*

The genus *Juncus* comprises more than 300 herbaceous, mostly perennial species with a nearly world-wide distribution (Kirschner *et al.*, 2002) and centres of diversity in the temperate zones. From central Europe about 30 species are known (Rothmaler, 2002) classified in two subgenera and seven different sections. Nine widespread species were selected from three larger sections: *Juncus acutiflorus, J. articulatus, J. atratus* and *J. bulbosus* from subgenus *Juncus* section *Ozophyllum*; *J. conglomeratus, J. effusus* and *J. inflexus* from subgenus *Agathryon* section *Juncotypus*; and *J. compressus* and *J. tenuis* from section *Steirochloa. Juncus tenuis* is not native to Europe but is now widespread there since its introduction from the early 19th century.

All the species selected are perennials and like most members of the genus they prefer quite similar habitat conditions like wet or seasonally flooded sites in open, often disturbed habitats and early successional stages. With the exception of the annual species (sections *Caespitosi* and *Tenageia*), a wide range of the phenotypic and phylogenetic diversity of *Juncus* species present in Central Europe was included in the study. Flowers of the *Juncus* species are wind-pollinated and slightly protogynous and anthesis is completed within 1 d. In some cases, anthesis even lasts only a few hours as in *J. tenuis* (Buchenau, 1892). *Juncus* spp. populations were investigated at six localities within the urban area of Halle (Saale), Germany (51°28'N, 11°58'E; Table 1). All populations were studied in the field except that of *J. atratus* which consisted of a set of plants grown in pots and raised from seeds that had been sampled from various populations in Germany. The natural populations comprised

TABLE 1. *The* Juncus *populations investigated and flowering descriptors*

| Species | Site* | Year | Flowering duration of population | Mean individual flowering | No. of pulses over one flowering period | Mean cycle length† [days (s.d.)] |
|---|---|---|---|---|---|---|
| *J. acutiflorus* | 1 | 2003 | 14 | 12·4 (1·9) | 5 | 2·8 (0·5) |
| *J. acutiflorus* | 1 | 2004 | 26 | 22·8 (2·1) | 6 | 4·4 (0·9) |
| *J. articulatus* pop 1 | 3 | 2004 | 42 | 33·0 (5·2) | Approx. 11, weak | 4·0 (1·8) |
| *J. articulatus* pop 2 | 1 | 2004 | 37 | 30·8 (3·4) | 8 | 4·3 (2·3) |
| *J. atratus* | 6 | 2004 | 22 | 14·8 (3·2) | 8 | 2·6 (0·5) |
| *J. bulbosus* | 1 | 2004 | 27 | 19·6 (8·2) | 6 | 4·8 (2·6) |
| *J. compressus* | 5 | 2003 | 7 | 3·8 (0·8) | 2 | 4·0 |
| *J. compressus* pop 1 | 2 | 2004 | 12 | 6·1 (1·7) | 3 | 3·5 (0·7) |
| *J. compressus* pop 2 | 1 | 2004 | 12 | 5·9 (2·2) | 3 | 4·0 (1·4) |
| *J. conglomeratus* | 1 | 2004 | 14 | 8·9 (2·5) | 4 | 3·7 (0·6) |
| *J. effusus* pop 1 | 4 | 2004 | 15 | 10·5 (2·9) | 4 | 4·0 (1·0) |
| *J. effusus* pop 2 | 3 | 2004 | 14 | 7·5 (2·6) | 4 | 4·0 (1·0) |
| *J. inflexus* | 2 | 2004 | 27 | 10·6 (5·4) | 6 | 4·8 (1·3) |
| *J. tenuis* | 1 | 2004 | 25 | 18·5 (6·4) | 5 | 4·7 (2·5) |

* Site 1: nature reserve at Brandberge, ruderalized wetland (latitude 51·513°, longitude 11·926°); site 2: Heide-Süd, ruderalized wetland (51·490°, 11·932°); site 3: Heide, edge of a seasonally flooded pond (51·498°, 11·920°); site 4: Galgenberg, seasonally flooded wetland (51·506°, 11·976°); site 5: nature reserve at Talstrasse, wet meadow (51·503°, 11·946°); site 6: artificial population held in pots (51·496°, 11·938°).

† Mean cycle length was defined as the average number of days between the flowering maxima.

hundreds to several thousand individuals covering areas of at least 200 $m^2$ up to 630 000 $m^2$. The minimum and maximum distances between populations were 1·3 km and 3·5 km, respectively.

### *Data collection*

In each population (Table 1) a number of stems ($n = 9–24$, mean 15·7) each belonging to a different individual plant and bearing one inflorescence was randomly marked. Thus, one stem was assumed as representative for the whole individual and possible variation among stems within an individual was neglected. All stems were marked several days before onset of flowering and irrespective of developmental stage. Then all marked plants were visited daily until the end of the population flowering period. The number of open flowers per individual $i$ and day $t$ ($x_i^t$) were counted or, if exceeding 100 (*J. atratus, J. effusus*), estimated. Opening of the flowers occurs before noon; therefore surveys were performed between 0900 and 1100 h.

To determine proximate environmental factors that may influence and synchronize the flowering phenology, at the same time as the phenological observations, temperature and humidity were recorded hourly in the flowering period of 2004 using a TinytagUltra data logger (Gemini Data Loggers Ltd, Chichester, UK). The device was installed under a white wooden shelter near the ground directly at site 1 where most populations were investigated (Table 1). Because all sites were close to each other, it is highly improbable that the environmental parameters recorded at site 1 were not representative of the other sites investigated. Daily precipitation records for the city of Halle were provided by the German National Meteorological Service (DWD, 2004).

### *Parameters of flowering phenology*

From the daily flowering records, the population flowering duration and the mean individual flowering duration which spanned the time from the first to the last day with open flowers at population and individual level, respectively, were determined. As rough descriptors of the flowering patterns, the number of flowering pulses which were defined by a local maximum of the number of open flowers per day and population, were estimated. Also the mean cycle length, given as the number of days between the flowering maxima, is reported.

To quantify the pulsed flowering phenology on the population level, day-to-day variability in flowering was assessed using the population-level coefficient of variation ($CV_p$, standard deviation/mean; eqn 1) of the total number of open flowers per day $t$ and population $p$ ($x_p^t$) calculated over $n$ days of the total flowering period of the population.

$$CV_p = \frac{\sqrt{\frac{1}{n-1} * \sum_{t=1}^{n} \left(x_p^t - \overline{x_p^t}\right)^2}}{\overline{x_p^t}} \qquad (1)$$

Here, $CV_p$ values are based on individuals as sampling units and thus reflect the daily variance in the number of open flowers per individual and an additional variance component arising from the individual × day interaction. Hence, in addition to the $CV_p$, within-individual variability was estimated by the coefficient of variation on the individual level ($CV_i$, eqn 1 and substituting $x_p^t$ and $\overline{x_p^t}$ by $x_i^t$ and $\overline{x_i^t}$, respectively) and averaged over all individuals within the population. In cases where individual variation was lacking the standard deviation was set to zero (*Pulsatilla vulgaris, Drosera anglica*, and null models).

Among-individual synchrony was estimated following Koenig *et al.* (2003) as the mean of all pairwise Pearson correlations coefficients ($r_i$) of the numbers of open flowers per day ($x_i^t$) of all individuals within a population. Here, in contrast to the calculation of the $CV_i$, dates outside the individual flowering period were treated not as missing data but as zeros and pairwise correlations between individuals were obtained for the whole flowering duration of the population. Otherwise the correlation between two individuals with only a small overlap could be high without representing actual synchrony.

To test their usefulness, other measures of among-individual synchrony were calculated that are based on overlap in flowering time and have been frequently applied in studies of flowering phenology were calculated. This allowed the comparison to published data sets. The widely used index $S_A$ (Augspurger, 1983; eqn 2), which is an extension of a formula given by Primack (1980) and determined for each individual, was calculated:

$$S_A = \left(\frac{1}{n-1}\right) \times \left(\frac{1}{f_i}\right) \times \sum_{j=1}^{n} e_{i \neq j} \qquad (2)$$

Here, the synchronization level $S_A$ of an individual $i$ is a function of the number of individuals in the population ($n$), the number of days the individual is flowering ($f_i$) and the number of days two individuals $i$ and $j$ ($i \neq j$) are flowering simultaneously ($e_i$). $S_A$ has been criticized for its dependence on flowering duration because the factor $1/f_i$ increases the level of synchrony when flowering duration decreases. Hence, as supported by Bolmgren (1998), an alternative measure of synchronization was introduced by Marquis (1988) ($S_M$; eqn 3). $S_M$ thus facilitates comparison between species irrespective of flowering duration. Furthermore, $S_M$ is a function of the numbers of open flowers per plant in contrast to Augspurger's measure $S_A$ which uses the mere information on whether a plant is flowering or not. $S_M$ accounts for full effects of variation in both the within-individual and the between-individual flowering patterns, and eventually includes the overlap of the individual flowering with the flowering of other individuals as an aspect of cross-fertilization (Bolmgren, 1998).

$$S_M = \sum_{t=0}^{n} \left( \frac{x_i^t}{\sum_{t=0}^{n} x_i^t} \right) \times p^t \qquad (3)$$

Here, $x_i^t$ is defined as above, $\Sigma x_i^t$ is the total number of flowers of individual $i$ during the whole flowering period and $p^t$ is the proportion of all marked stems in bloom at day $t$. Thus, maximum synchrony is reached when within-individual flowering is synchronized and coincides with the flowering events of other individuals in the population (Bolmgren, 1998). Both measures ($S_A$ and $S_M$) were first calculated on the individual level and then averaged over all individuals of the population. They can range between zero and one (maximal synchrony).

For comparison, all above-mentioned parameters were also calculated for two further species published phenological data. First, as representative of the most common pattern of unimodal flowering (cornucopia type) *Pulsatilla vulgaris* (Kratochwil, 1988), which exhibits long-lasting flowers, was used. Secondly, *Drosera anglica* (Murza and Davis, 2005; G. L. Murza, Department of Biology, University of Saskatchewan, pers. com.), showing variable flowering and very short-lived (1 d) flowers, was used. Unfortunately, it was not possible to calculate $CV_p$ and $CV_i$ for more species for which parameters of synchrony (e.g. $S_A$) have been published due to a lack of data on individual flowering in high temporal resolution.

### *Null models and randomization tests*

To test for differences among populations and to estimate the variability of the parameters $CV_p$, $CV_i$, $r_i$ and $S_M$ confidence limits for each population were obtained by bootstrapping 1000 times with individual plants as units of resampling.

To test whether the observed flowering pattern deviates from a random pattern, range-constrained null models were constructed on the individual level. First, the flowering onset of each individual within the population flowering time was randomly altered. Neither the individual nor the population flowering duration was changed by this step. Secondly, the total number of open flowers per individual was randomly distributed within the individual flowering days. For *Pulsatilla*, whose flowers remain functional for several days, the randomization step was accomplished by randomly shifting the flowering of each flower within the individual flowering duration, without altering the flowering duration of the flower. For each population 1000 null models were generated and parameters calculated. A parameter was considered significant if there was no overlap between 95 % of the values derived from the null models and the 95 % confidence interval obtained from bootstrapping the original data set.

To analyse the performance of the parameters $CV_p$, $CV_i$, $r_i$ and $S_M$ and their relationship among each other the flowering of a population was simulated and the flowering behaviour of its individuals varied. The population modelled consisted of 15 individuals each producing 140 flowers over a total flowering period of 25 d, similar to the species investigated. At the starting point synchrony was at its maximum with all plants flowering each fourth day for seven times (day 1, 5, 9, 13, 17, 21 and 25) with 20 flowers per plant per flowering day. Since all individuals showed the same flowering pattern the population-level $CV_p$ equalled the within-individual $CV_i$. Starting from this point the individual flowering behaviour was varied in two different ways as follows.

(1) The position of the individual flowering pulses was varied keeping constant the number of pulses and the number of open flowers per flowering pulse. The position of each flowering pulse was allowed to vary within $\pm 2$ d of the original flowering date. In the course of the simulation the randomness for the position of the flowering date within this range was increased stepwise by drawing each flowering date from a normal distribution with a mean of zero and a standard deviation varying between 0 (minimum) and 1·5 (maximum randomisation). For example, at the point of maximum randomization the flowering pulse originally at day 5 could occur on all days between days 3 and 7 with equal chance. By this procedure the mean individual flowering duration was unchanged and the within-individual variability should be largely unaffected. However, the synchrony among individuals should decrease.

(2) An increasing proportion of the original flowers of each individual was randomly distributed over the 25 d of the flowering period. In the first step, 5 % of an individual's 140 flowers were randomly distributed over the flowering period. The remaining 95 % flowered equally distributed on the original flowering days. Thus, with increasing randomization the concerted maxima of flowering on days $1, 5 \ldots 25$ were flattened towards a uniform distribution of flowers randomly distributed. By this approach the within-individual variability in flowering will be decreased, which will also affect the population-level variability. However, among-individual synchrony, as measured by flowering overlap ($S_M$), should be less affected.

### *Correlation analyses*

The importance of within-individual variability and among-individual synchrony for $CV_p$ was analysed by Pearson correlation analyses between $CV_p$ and $CV_i$, $r_i$, $S_M$ and $S_A$ separately and by multiple linear regression of $CV_p$ on $CV_i$ and $r_i$, $S_M$ or $S_A$ with stepwise backward selection. Testing the hypothesis that selection may act independently on both within-individual variability and among-individual synchrony, the correlation between $CV_i$ and each of the synchrony measures was evaluated.

Values for all parameters were used from all observed *Juncus* populations, *Pulsatilla vulgaris* and *Drosera anglica*. All variables did not deviate significantly from normal distribution (see Results). Several species were assessed in two successive years or were observed in two populations and entered more than once into the analysis and thus may have introduced a potential bias. However, repeated analyses using only one data set per species revealed nearly identical results. Several measures of among-individual synchronization were computed. To test whether $r_i$, $S_M$ and $S_A$ are mutually replaceable, Pearson correlation analyses were performed.

It has been argued that values of species traits cannot be treated as independent points in comparative analyses (Harvey and Purvis, 1991). To account for possible confounding effects of the phylogenetic relationship among the species, all analyses were repeated using phylogenetic independent contrasts (PIC) (Felsenstein, 1985). PIC values cannot be assigned to a distinct species but rather reflect the evolution of a trait within a clade. PIC data were calculated using the CAIC software package (Purvis and Rambaut, 1995) with the implemented 'crunch' algorithm and branch lengths of the phylogenetic tree set to unity. Phylogenetic information for the cladogram used to compute the PIC data was extracted from Drabkova *et al.* (2006). Additional information was derived from nrDNA external transcribed spacer sequence data of the *Juncus* species studied (S. G. Michalski, unpubl. res.). Regression and correlation routines to analyse PIC data were forced through the origin as stated in detail by Garland *et al.* (1992).

To test for possible environmental cues for the population-wide flowering pulses, temperature, humidity and precipitation data were correlated with the total number of open flowers per day, separately for each population. The flowering duration of an individual is usually shorter than that of the whole population. Hence, the total number of open flowers at the beginning and at the end of the population flowering duration is lower than the one in-between those dates. This fact may lower the significance of an existent relationship with an environmental factor. An attempt was made to compensate for this effect by dividing the total number of open flowers per population by the number of inflorescences in flower on that day and using these data in the analyses. For the correlation analysis, the following parameters were derived from the hourly logged temperature and humidity data: averaged temperature ($T$) and humidity ($h$) values over 24 h ($T_{24}$ and $h_{24}$) and over 6 h ($T_6$ and $h_6$) prior to the census (1000 h); maximum temperature ($T_{max}$) and minimum humidity ($h_{min}$) of 24 h before the census. Because a delayed reaction of flowering caused by temperature or humidity is possible, averaged values of 24 h, 2 d prior to the census, were also included in the analysis ($T-1$ and $h-1$). If flowering is dependent of internal conditions (e.g. growth rate and resource allocation), heat sums over a longer period rather than single-day conditions might explain the flowering pattern. Hence, hourly logged temperature values were summarized over 120 h prior to the census and included in the analysis ($T_{120}$). Additionally, the total precipitation of the day before the census was included. All relationships between flowering and environmental parameters were evaluated using Pearson correlations. The total number of open flowers per day is not necessarily independent of the number on the next day. Hence, the statistical significance of the relationships was evaluated by testing the correlation coefficient against a distribution of correlation coefficients obtained by correlating the original flowering data with the environmental data randomized across days (1000 permutations, $\alpha = 0{\cdot}05$, two-sided). All statistical analyses were performed with R 2·3·1 (R Development Core Team, 2006).

## RESULTS

### *Patterns of flowering phenology*

The total flowering duration ranged from 7 d to 42 d among populations. All *Juncus* populations showed a more or less pronounced pulsed flowering phenology (Fig. 1A–I). In populations of *J. acutiflorus, J. atratus, J. conglomeratus, J. effusus* and *J. tenuis* flowering pulses were highly synchronized among marked inflorescences. Flowering episodes of 1 or 2 d were separated by days without or with very few open flowers. *Juncus tenuis* showed gaps between these flowering events of up to 6 d (Fig. 1H). Depending on the species, 2–11 of such population-wide events or pulses could be observed over the flowering period (Table 1). Individual stems sometimes showed only one distinct event (*J. conglomeratus*, and very pronounced in *J. effusus*) at which almost all flowers of the inflorescence opened up simultaneously on one day. In some populations not all marked stems flowered in all pulses. However, the first flowering pulse of younger inflorescences coincided with later-flowering episodes of more mature stems (e.g. *J. inflexus*). The least distinct pulses were seen in populations of *J. articulatus* and *J. compressus*.

The population-level coefficient of variation of all *Juncus* populations was significantly higher than that of constantly flowering species with unimodal flowering phenology as displayed by *Pulsatilla vulgaris* ($CV_p = 0{\cdot}70$; Table 2). Values of $CV_p$ ranged from a more constant flowering as in *J. compressus* (0·89 in 2003) and *J. articulatus* (1·04, pop 1) to highly synchronous pulsed flowering as in *J. effusus* (2·78, pop 1). Also, the within-individual variability in the number of open flowers ($CV_i$) was significantly higher than for unimodal flowering ($CV_i = 0{\cdot}17$ for *Pulsatilla vulgaris*). $CV_i$ ranged from 0·77 in *J. compressus* (2003) to 2·53 for *J. tenuis* (2·53).

The synchronization level as measured by several parameters ($r_i$, $S_A$ and $S_M$) varied 2- to 3-fold among *Juncus* species (Tables 2 and 3). Lowest values for among-individual synchrony were found for *J. inflexus* (e.g. $S_M = 0{\cdot}43$), highest values for *Juncus acutiflorus* (2004, $S_M = 0{\cdot}95$; Table 2). *Drosera anglica* showed a similar degree of variability in flowering as the *Juncus* species but differed by exhibiting very low levels of among-individual synchrony.

With the exception of population 2 of *J. compressus* (2004) all $CV_p$ and $CV_i$ values for the *Juncus* species studied and for *D. anglica* were significantly different from a random phenology (Table 2). Also among-individual synchrony as measured by $r_i$ was significantly different from random, except for the populations of *J. compressus*. However, when among-individual synchrony was measured by $S_M$ only, populations of *J. effusus, J. tenuis* and *D. anglica* showed significant values when tested against a random flowering. *Pulsatilla vulgaris*, representing a unimodal flowering pattern, showed no deviation from random for all parameters.

### *Simulated phenologies*

To analyse the performance of the flowering parameters the individual flowering behaviour was altered in two

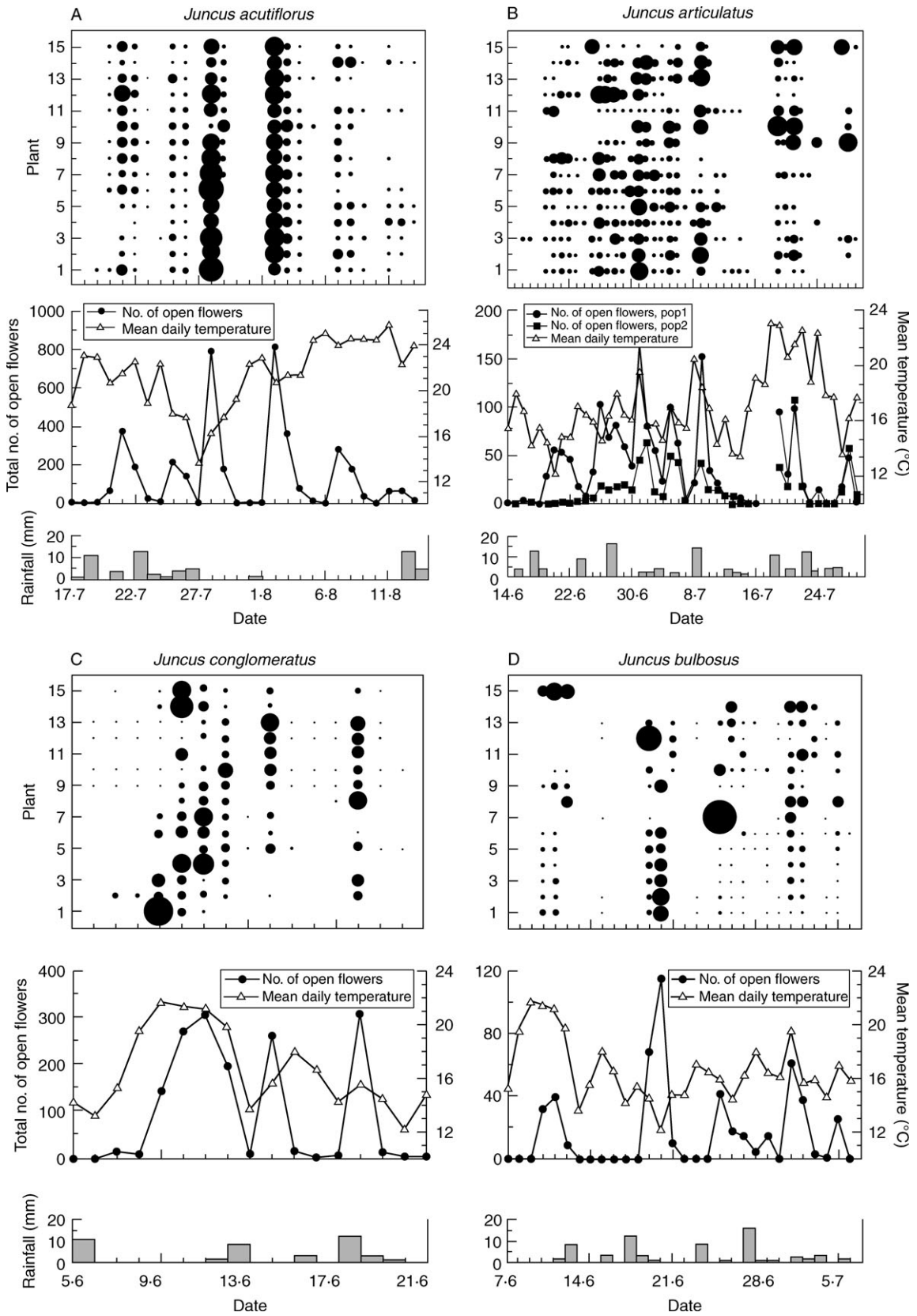


FIG. 1. (A–I) Flowering phenology of nine *Juncus* species on individual inflorescence- and population-level in comparison to daily mean temperature and precipitation in 2004. The size of the dots is proportional to the relative number of open flowers on that day for each marked stem. In the dot-plots only 15 plants from one population are depicted.

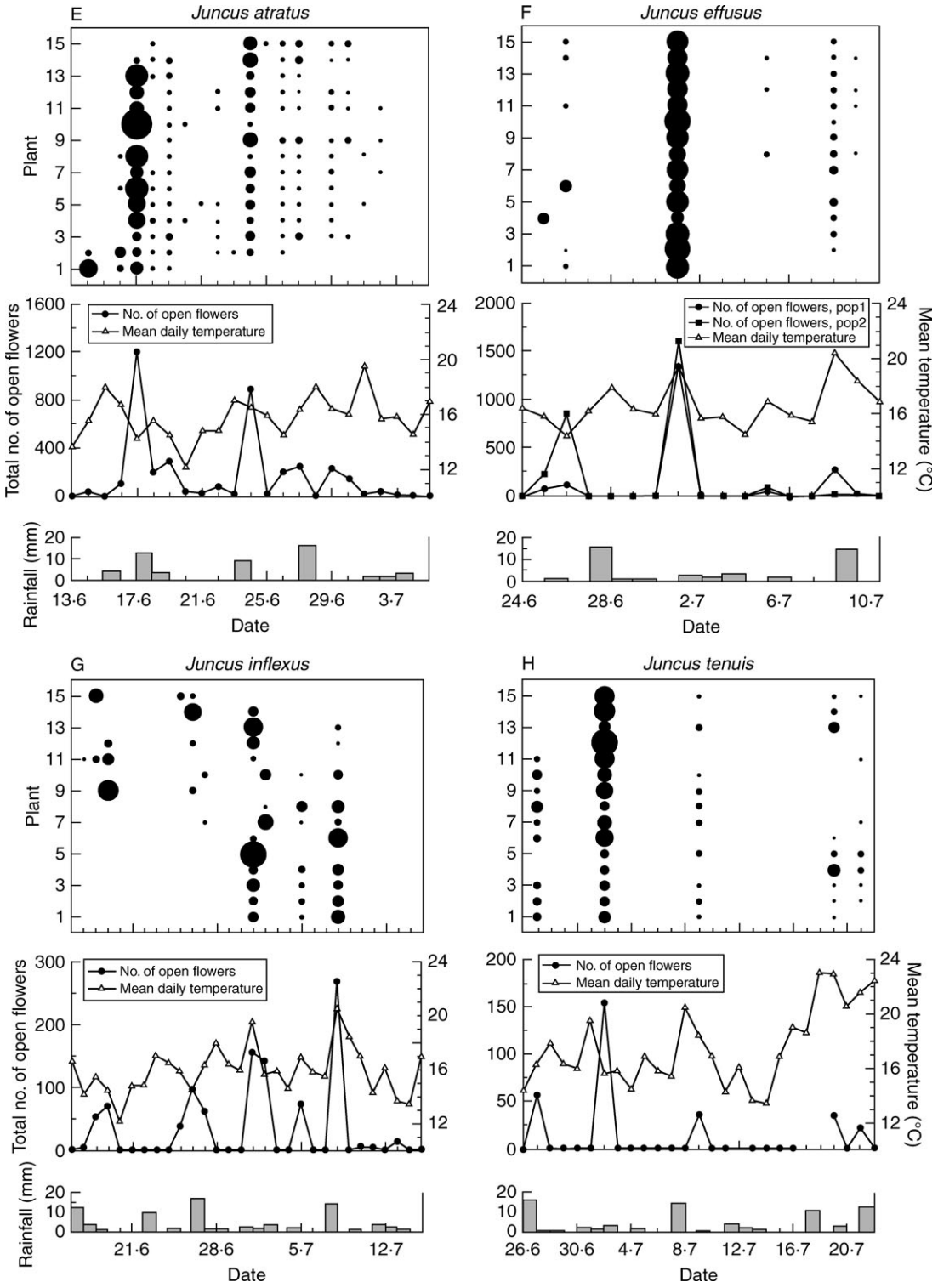


FIG. 1. Continued.

ways. In simulation (1), in which the randomness in the date of the flowering pulses was increased, as expected, $CV_i$ was only slightly decreasing (Fig. 2). Both synchrony measures were nearly equally responsive to the altered individual flowering and were decreasing continuously with increasing randomness. The decreasing synchrony among individuals was also reflected in a decreasing $CV_p$, which contrasts to the performance of the individual variability $CV_i$.

In simulation (2), in which an increasing proportion of the original number of open flowers of all individuals was

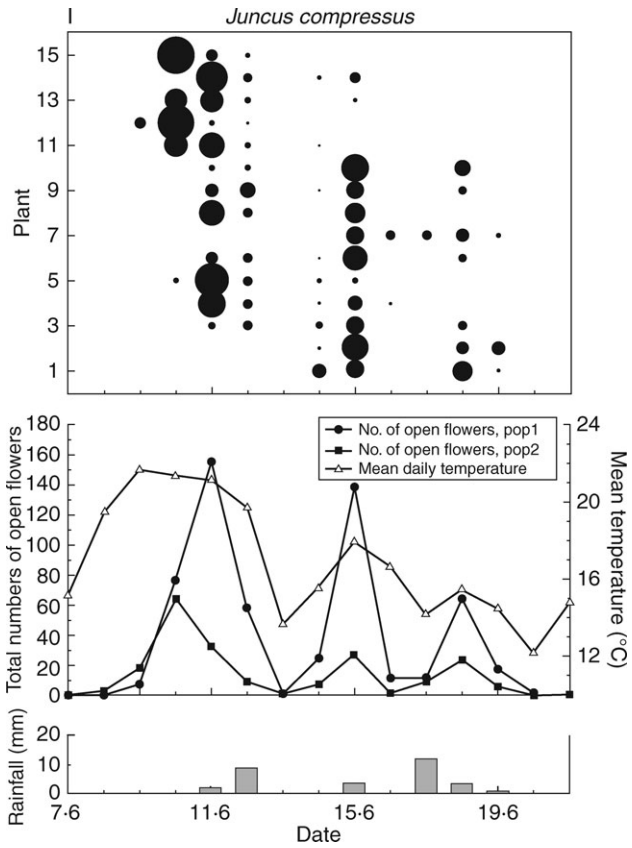


FIG. 1. Continued.

randomly distributed among all flowering days, $S_M$ values stayed nearly constant over the whole simulation. $CV_p$, $CV_i$ and $r_i$ were continuously decreasing with an increasing proportion of flowers randomized (Fig. 2). Whereas $CV_p$ and $CV_i$ decreased linearly and thus were equally sensitive to less variable flowering, $r_i$ showed only a slight decrease at the beginning of the simulation and dropped much faster at approx. 50 % randomly distributed flowers.

Out of the four parameters used, only $CV_p$ was equally responsive in the two simulations.

### *Relationships among phenological measures*

Distributions of all parameters ($CV_p$, $CV_i$, $r_i$, $S_M$ and $S_A$) did not deviate significantly from normality (Shapiro-Wilk, $P > 0{\cdot}08$, for all parameters). Correlation analyses revealed a large contribution of $CV_i$ to $CV_p$ ($r = 0{\cdot}911$, $P < 0{\cdot}001$). Among-individual synchrony measures were strongly correlated with each other ($r_i$ and $S_A$: $r = 0{\cdot}76$, $P < 0{\cdot}001$; $r_i$, and $S_M$: $r = 0{\cdot}86$, $P < 0{\cdot}001$; $S_A$ and $S_M$: $r = 0{\cdot}96$, $P < 0{\cdot}001$). No significant relationships were found between $CV_p$ and $S_M$ or $S_A$ ($P > 0{\cdot}59$). However, the correlation of $CV_p$ with $r_i$ was marginally significant ($r = 0{\cdot}479$, $P = 0{\cdot}061$). The individual-level measure of variability ($CV_i$) was not related to any of the synchrony parameters ($P > 0{\cdot}13$). Multiple regressions of $CV_p$ on $CV_i$ and on one of the parameters $r_i$, $S_M$ or $S_A$ revealed statistically significant effects only for $CV_i$ ($t > 7{\cdot}22$, $P < 0{\cdot}001$) and no measure of among-individual synchronization was retained in the final model (adjusted $R^2 = 0{\cdot}819$, $P < 0{\cdot}001$).

A repeated analysis of the relationships using phylogenetic independent contrasts ($n = 11$) revealed essentially the same results as above (e.g. PIC regression of $CV_p$ on $CV_i$: adjusted $R^2 = 0{\cdot}867$, $P < 0{\cdot}001$; other results not shown). This indicates that relationships among the phenological measures are independent of phylogenetic patterns.

### *Relationships of flowering with environmental data*

Only nine out of 120 correlations between the total number of open flowers per day and environmental

TABLE 2. *Coefficient of variation of flowering at population ($CV_p$) and individual level ($CV_i$) and two measures of among-individual synchronization ($r_i$ and $S_M$) in populations of various* Juncus *species,* Pulsatilla vulgaris *(calculated from Kratochwil, 1988) and Drosera anglica (data provided by G. L. Murza, Department of Biology, University of Saskatchewan, pers. com. 2005)*

| Species | Year | *n* stems | $CV_p$ (95 % CI) | Mean $CV_i$ (95 % CI) | Mean $r_i$ (95 % CI) | Mean $S_M$ (95 % CI) |
|---|---|---|---|---|---|---|
| *J. acutiflorus* | 2003 | 10 | 1·22 (1·09–1·48)* | 1·36 (1·16–1·60)* | 0·80 (0·75–0·89)* | 0·93 (0·90–0·99) |
| *J. acutiflorus* | 2004 | 15 | 1·49 (1·40–1·63)* | 1·47 (1·38–1·57)* | 0·83 (0·78–0·91)* | 0·95 (0·94–0·98) |
| *J. articulatus* pop 1 | 2004 | 15 | 1·04 (0·94–1·19)* | 1·24 (1·08–1·38)* | 0·43 (0·37–0·59)* | 0·80 (0·75–0·87) |
| *J. articulatus* pop 2 | 2004 | 10 | 1·26 (1·15–1·50)* | 1·59 (1·36–1·84)* | 0·50 (0·45–0·68)* | 0·79 (0·75–0·86) |
| *J. atratus* | 2004 | 18 | 1·70 (1·47–1·94)* | 1·63 (1·49–1·79)* | 0·64 (0·53–0·78)* | 0·86 (0·79–0·95) |
| *J. bulbosus* | 2004 | 15 | 1·53 (1·29–1·80)* | 1·68 (1·39–1·94)* | 0·32 (0·23–0·55)* | 0·60 (0·49–0·77) |
| *J. compressus* | 2003 | 20 | 0·89 (0·74–1·12)* | 0·77 (0·61–0·94)* | 0·35 (0·22–0·50) | 0·72 (0·67–0·81) |
| *J. compressus* pop 1 | 2004 | 15 | 1·13 (0·91–1·40)* | 1·15 (1·08–1·24)* | 0·34 (0·25–0·57) | 0·64 (0·56–0·79) |
| *J. compressus* pop 2 | 2004 | 9 | 1·09 (0·79–1·65) | 0·90 (0·75–1·04)* | 0·23 (0·15–0·59) | 0·61 (0·51–0·84) |
| *J. conglomeratus* | 2004 | 20 | 1·19 (1·14–1·36)* | 1·30 (1·19–1·42)* | 0·44 (0·36–0·56)* | 0·81 (0·74–0·90) |
| *J. effusus* pop 1 | 2004 | 15 | 2·78 (2·52–2·94)* | 2·36 (2·15–2·56)* | 0·92 (0·86–0·98)* | 0·90 (0·85–0·96)* |
| *J. effusus* pop 2 | 2004 | 17 | 2·35 (2·06–2·82)* | 2·06 (1·84–2·32)* | 0·64 (0·54–0·84)* | 0·86 (0·80–0·94)* |
| *J. inflexus* | 2004 | 24 | 1·78 (1·61–2·17)* | 1·97 (1·55–2·03)* | 0·25 (0·19–0·41)* | 0·43 (0·36–0·58) |
| *J. tenuis* | 2004 | 17 | 2·54 (2·24–2·89)* | 2·53 (2·00–2·73)* | 0·71 (0·58–0·85)* | 0·78 (0·71–0·87)* |
| *P. vulgaris* | 1988 | 30 | 0·70 (0·43–0·73) | 0·17 (0·08–0·26) | 0·62 (0·42–0·84) | 0·83 (0·72–0·94) |
| *D. anglica* | 2000 | 23 | 1·41 (1·12–1·79)* | 0·99 (0·68–1·29)* | 0·20 (0·13–0·38)* | 0·33 (0·27–0·48)* |

Asterisks (*) indicate a significant deviation from temporally random individual flowering.

TABLE 3. *Augspurger's synchrony measure ($S_A$) for 41 species.* Juncus *species are scattered throughout the whole spectrum and marked with an asterisk (*)*

| Species | $S_A$ | Reference |
|---|---|---|
| *Faramea picinguabae* | 0·32 | SanMartin-Gajardo and Morellato, 2003 |
| *Drosera anglica* | 0·32 | Murza and Davis, 2005 |
| *Couratari multiflora* | 0·35 | Lepsch-Cunha and Mori, 1999 |
| *Photinia davidiana* | 0·35 | Kudo and Suzuki, 2004 |
| *Vaccinium stapfianum* | 0·35 | Kudo and Suzuki, 2004 |
| *Juncus inflexus** | 0·39 | This study |
| *Pentagonia macrophylla* | 0·48 | Augspurger, 1983 |
| *Psychotria leitana* | 0·49 | SanMartin-Gajardo and Morellato, 2003 |
| *Erythrina costaricensis var. panamensis* | 0·50 | Augspurger, 1983 |
| *Ferocactus cylindraceus* | 0·50 | McIntosh, 2002 |
| *Juncus compressus* (2004, pop2)* | 0·51 | This study |
| *Ranunculus dissectifolius* | 0·53 | Pickering, 1995 |
| *Psychotria pupigera* | 0·53 | SanMartin-Gajardo and Morellato, 2003 |
| *Rhododendron buxifolium* | 0·53 | Kudo and Suzuki, 2004 |
| *Juncus bulbosus** | 0·56 | This study |
| *Juncus compressus* (2004, pop1)* | 0·59 | This study |
| *Ranunculus muelleri* | 0·59 | Pickering, 1995 |
| *Rhododendron ericoides* | 0·60 | Kudo and Suzuki, 2004 |
| *Rudgea jasmininoides* | 0·61 | SanMartin-Gajardo and Morellato, 2003 |
| *Ranunculus graniticola* | 0·63 | Pickering, 1995 |
| *Juncus compressus* (2003)* | 0·66 | This study |
| *Juncus effusus* (pop1)* | 0·66 | This study |
| *Ranunculus millanii* | 0·67 | Pickering, 1995 |
| *Juncus articulatus* (pop1) * | 0·68 | This study |
| *Psychotria birotula* | 0·68 | SanMartin-Gajardo and Morellato, 2003 |
| *Juncus tenuis** | 0·70 | This study |
| *Silene acutifolia* | 0·70 | Buide *et al.*, 2002 |
| *Chromolaena odorata* | 0·70 | Almeida-Neto and Lewinsohn, 2004 |
| *Juncus atratus** | 0·72 | This study |
| *Juncus effusus* (pop2)* | 0·72 | This study |
| *Juncus articulatus* (pop1)* | 0·73 | This study |
| *Ranunculus niphophilus* | 0·73 | Pickering, 1995 |
| *Juncus conglomeratus** | 0·74 | This study |
| *Lotus corniculatus* | 0·74 | Ollerton and Lack, 1998 |
| *Leptospermum recurvum* | 0·74 | Kudo and Suzuki, 2004 |
| *Psychotria nuda* | 0·75 | SanMartin-Gajardo and Morellato, 2003 |
| *Pulsatilla vulgaris* | 0·76 | Kratochwil, 1988 |
| *Turnera panamensis* | 0·77 | Augspurger, 1983 |
| *Ferocactus wislizeni* | 0·79 | McIntosh, 2002 |
| *Hormatophylla spinosa* | 0·82 | Gómez, 1993 |
| *Psychotria horizontalis* | 0·82 | Augspurger, 1983 |
| *Juncus acutiflorus* (2003)* | 0·84 | This study |
| *Rudgea vellerea* | 0·85 | SanMartin-Gajardo and Morellato, 2003 |
| *Juncus acutiflorus* (2004)* | 0·86 | This study |
| *Hybanthus prunifolius* | 0·89 | Augspurger, 1983 |
| *Rinorea sylvatica* | 0·95 | Augspurger, 1983 |

data showed a significant relationship. Flowering of *J. compressus* (pop 1, 2004, $T_{24}$, $r = 0{\cdot}71$, $T_6$, $r = 0{\cdot}78$; pop 2, 2004, $T_6$, $r = 0{\cdot}61$) and *J. conglomeratus* ($T_{24}$, $r = 0{\cdot}58$; $T_6$, $r = 0{\cdot}52$; $T_{max}$, $r = 0{\cdot}66$) was significantly and positively related to temperature ($T$). Humidity was significantly negatively correlated in *J. effusus* ($h_6$, $r = -0{\cdot}53$) and *J. articulatus* (pop 2; $h-1$, $r = -0{\cdot}33$). However, by controlling the overall type I error rate using Bonferroni correction only one correlation remained significant (*J. compressus* pop 1, 2004, $T_6$)

As can be expected, environmental parameters were partly intercorrelated; in particular, humidity ($h$) and precipitation, humidity of the day before ($h-1$) and precipitation, and most parameters derived from temperature ($T$) with each other. However, reducing the climatic variation by principal component analysis to one or two factors and using these factors for correlation analysis with flowering data revealed no significant relationships (data not shown).

## DISCUSSION

Most of the *Juncus* populations studied exhibited a highly variable flowering pattern expressed in population-wide flowering pulses. The population-wide flowering pulses were mainly based on the temporal variability in flowering of the individuals. Some populations even showed a highly synchronized pulsed flowering that as far as is known is the only recorded case for herbaceous plants. However, many studies in flowering phenology do not report the flowering of a species on a daily basis and thus may have missed a potentially existent variability in flowering on individual and population levels.

Only four cases were found in the literature in which a similar flowering phenology has been described, all from woody species from the Brazilian Cerrados. *Myrica rhodosepala, Blepharocalyx salicifolius* (Proença and Gibbs, 1994) and *Myrica tomentosa* (Torezan-Silingardi and de Oliveira, 2004), all trees and members of the Myrtaceae, showed up to three distinct flowering pulses within 8–35 d. Many more pulses, scattered over a 3-month period, were observed in *Vellozia squamata* (Velloziaceae), a woody shrub (Oliveira *et al.*, 1991). As in *Juncus*, anthesis is short in these species and the duration of single pulses varies between 1 and 3 d. Irrespective of these common characteristics all previous examples are insect-pollinated, woody species, most of which possess a self-incompatibility system (*M. rhodosepala* is self-compatible) in contrast to *Juncus* which is self-compatible and pollinated by wind.

### *Descriptive parameters of flowering phenology*

The description of flowering patterns and the analysis of selective influences requires measures that reflect all aspects of flowering on individual and population levels. In species with highly variable flowering, as in *Juncus*, traditional measures like duration of the flowering period or among-individual synchrony do not fully describe the temporal patterns observed. By only taking these into account the most common unimodal flowering pattern cannot be distinguished from a pulsed flowering (e.g. $S_A$; Table 3).

Thus, applying one of the CV values as a descriptive parameter of flowering phenology is an adequate way to estimate temporal variability in flowering patterns. It also allows the comparison of different flowering phenologies, particularly in combination with an adequate measure of among-individual synchrony. By this combination of

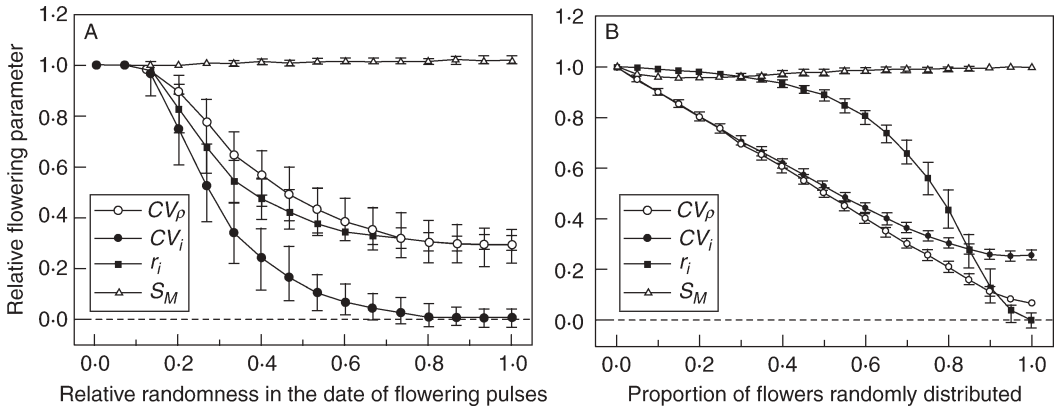


FIG. 2. Relative performance of the descriptive parameters $CV_p$, $CV_i$, $r_i$ and $S_M$ for a theoretical population with varying individual flowering behaviour. The dataset was altered starting from a strict population-wide pulsed flowering ($CV_p = 1{\cdot}64$, $CV_i = 1{\cdot}64$, $r_i = 1{\cdot}0$ and $S_M = 1{\cdot}0$). In (A) the randomness for the date of the flowering pulses was increased. Maximum randomness was achieved when individuals flowered randomly within $\pm 2$ d of the original flowering day. Note the constant individual variability $CV_i$ and the decreasing measures of synchrony and population variability $CV_p$. In (B) for each individual in the population an increasing proportion of flowers was randomly spread over the individual's flowering period. This affects the synchrony measures in different ways, while variability on individual and population levels respond equally.

parameters *Juncus* species are separated from unimodal peak flowering patterns typical for 'mass flowering' or 'cornucopia' type phenologies as represented here by *Pulsatilla vulgaris* which has low CV values due to low variation in flowering. The *Juncus* species investigated here may be roughly grouped into species with strongly synchronized pulsed flowering like *J. effusus, J. tenuis, J. atratus* and *J. acutiflorus* (high CV and high synchrony) and those displaying only weakly synchronized pulsed flowering (high CV and low synchrony). For the *Juncus* species, represented by more than one population, the measures of temporal variability and synchrony both varied among populations and years. However, based on the 95 % confidence limits several species clearly differed in the extent of synchronous pulsed flowering (Table 2).

The extent of variability and synchrony was quite independent from phylogenetic relationships among the *Juncus* species investigated. For example, the closely related *J. effusus* and *J. conglomeratus* clearly differed in these flowering parameters, while the related species pair *J. atratus* and *J. acutiflorus* showed a similar flowering behaviour (Table 2).

The biological importance of the population-level parameter $CV_p$ is hard to assess. Referring to mast seeding data sets, Herrera (1998) suggested the dissection of the $CV_p$ into biologically more relevant parameters of within-individual variability and among-individual synchrony. In fact, analysis of mast seeding data showed that temporal variation on population-level ($CV_p$) reflected both, variation in $CV_i$ and, to a lesser extent, variation in among-individual synchrony (Herrera, 1998; Koenig *et al.*, 2003). By using the same parameters to describe the flowering of *Juncus* ssp. within one flowering period this relationship could not be validated. Here, variation of $CV_p$ among species was only due to variation of $CV_i$ and not due to variation of among-individual synchrony. This substantiates the fact that $CV_p$ alone is not sufficient to describe all components of a flowering pattern. This fact was also supported by the simulation study. The performance of $CV_p$ was quite similar for the two cases modelled, although in one case the flowering pulses of individuals were disordered, resulting in decreased synchrony, whereas in the second case synchrony was nearly kept constant (see $S_M$) when an increasing proportion of all open flowers was randomized.

In neither the present data on flowering patterns nor in data on mast flowering (Herrera, 1998; Koenig *et al.*, 2003) was a significant relationship between $CV_i$ and among-individual synchrony detected. From this finding, Koenig *et al.* (2003) concluded that the two components of population-level variability may be independent under selection. For mast flowering, they also suggested that in particular wind-pollination is a factor which selects for both within-individual variability and synchrony. This is also applicable to flowering patterns within a flowering period, as is discussed below.

In the present study, several parameters, which measure among-individual synchrony, were used. However, the simulations showed that $r_i$, and $S_M$ can perform quite differently (Fig. 2B). Although in one simulation (Fig. 2B) all individuals flowered in synchrony, $r_i$, in contrast to $S_M$, was affected by the increasing component of chance with increasing proportion of flowers randomly distributed. This discrepancy between the synchrony measures was also detected in the real data, as for example in *J. articulatus* which had a low $r_i$ but high $S_M$ (pop 1, Table 2).

All relationships among the flowering parameters investigated were not different for the original data and for phylogenetic independent contrasts. Hence, phylogenetic relatedness seems not to confound the results obtained. However, the sample size might be too small to derive definite conclusions.

### *Proximate causes of pulsed flowering*

For most of the *Juncus* populations studied, no clear influence of environmental factors on population-wide

flowering could be demonstrated. In the study of Proença and Gibbs (1994) one of the two species with a pulsed flowering phenology showed a coincidence of a strong increase of humidity and flowering. Flowering in *Juncus* species has been described as promoted by elevated temperature and in some species, as for example for *J. compressus*, also by high levels of humidity (Graebner, 1934). Indeed, in particular for the populations of *J. compressus* temperature was correlated with flowering, although after controlling for the type I error only one case remained significant. However, neither air humidity nor precipitation was found to exert an influence on the flowering patterns. In concordance with the descriptions of Buchenau (1892), single flowering events sometimes even coincided with rain, a condition very unfavourable for wind-pollination.

For three *Juncus* species, two populations each were investigated in 2004. The flowering patterns between the three population pairs were highly correlated in all cases ($r > 0{\cdot}65$, permutation $P < 0{\cdot}05$; see also Fig. 1B, F, I) suggesting that the flowering patterns were the result of shared environmental cues. This among-population correlation was found for species with pronounced (*J. effusus*) or weak synchronous pulses (*J. compressus, J. articulatus*).

Nevertheless, a potential influence of environmental factors on flowering phenology is hard to detect in natural populations. The flowering period of a single population provides only few data points limiting the significance of any analysis. Furthermore, different *Juncus* species may also act differently. More evidence for environmental cues could be supplied by collecting environmental and flowering data for many natural populations of the same species over one flowering period or by conducting experiments with artificial populations under controlled environmental conditions.

### *Ultimate causes of synchronous pulsed flowering*

Mechanisms that may be involved in the selection and maintenance of flowering synchrony are not necessarily the same as for the selection and maintenance of the flowering pulses. Accordingly, the present results showed that among-individual synchrony (e.g. $S_M$) and within-individual variability ($CV_i$) are not related. Maximum synchrony could also be achieved by a single, short-lasting flowering event without expending the reproductive effort in pulses. Examples for such a 'big bang' strategy have been frequently described from tropical or subtropical species (e.g. Gentry, 1974; Augspurger, 1983; Proença and Gibbs, 1994).

A number of mutually non-excluding factors may contribute to pulsed flowering. First, physiological or developmental constraints may limit the number of flowers open at one time. Buchenau (1892) considered that the degree of bud maturation is an important factor for pulsed flowering. He noticed that the temporal order of the opening of individual flowers within an inflorescence can be quite variable for different inflorescence architectures. However, there is no clear relationship between the degree of pulsing and inflorescence architecture, since compact (*J. conglomeratus, J. effusus, J. inflexus*), loose (*J. acutiflorus, J. atratus, J. compressus*) and dispersed (*J. bulbosus, J. articulatus, J. tenuis*) inflorescence types showed no consistent pulsing patterns within their group.

In contrast to a short unimodal flowering event, pulsed flowering might be interpreted as an extended flowering pattern that can confer several advantages. It was proposed that an extended flowering period should allow a better control of the relative investment in flowers and fruits (Bawa, 1983). Thus, the pulsed flowering could be a strategy to match resource demands over time. It has also been found that extended flowering or multiple reproductive events within a season can be advantageous for seed production because late or less dense flowers could escape seed predation (e.g. Eriksson, 1995; Pico and Retana, 2000). However, although predispersal seed predators are known for *Juncus* (e.g. Randall, 1986) this explanation seems unlikely for *Juncus*, because the times between the flowering pulses are too short to allow a significant variability in seed production.

The dependency of wind-pollination on favourable weather conditions itself could explain selection for a pulsed flowering. In accordance to Buchenau (1892), sometimes flowering inflorescences were observed dripping wet from rain, which hardly enables wind-pollination. Hence, it might be more beneficial to spread the flowering effort over several occasions in order to encounter adequate environmental conditions at least during one flowering pulse. A single flowering event would always risk reproductive failure due to bad weather conditions. Thus, pulsed flowering could also be interpreted as a risk spreading strategy. Theoretical studies have shown that risk-spreading adaptations or bet-hedging of generative and reproductive expenditures can be favourable strategies in unpredictable environments (Yoshimura and Clark, 1991; Wilbur and Rudolf, 2006). However, when the plant cannot anticipate favourable conditions for pollination from environmental cues, a random opening of flowers across the season would also be a risk-spreading strategy. For example, the extended flowering duration of the palm *Geonoma epetiolata* has been interpreted as an adaptation to increase the chances of reproduction in an environment with high and unpredictable rainfall (Marten and Quesada, 2001). Such a uniform scattering of the reproductive effort across the flowering period can also result in high among-individual synchrony as a premise for cross-pollination (see Fig. 2). Hence, for *Juncus* species the enhanced flower density at individual and population level during the pulses must be beneficial too.

The effects of floral density caused by the pulses have to be considered in relation to wind pollination. A higher flower density and hence a higher pollen density at individual level is likely to increase geitonogamy which may cause decreased female fitness in outcrossing taxa due to a higher proportion of self pollen on the stigmas. On the other hand, the male fitness gain in wind-pollinated plants is not expected to decrease with an enhanced floral display. For instance, in contrast to animal-pollinated plants, in wind-pollinated plants the pollen vector cannot be saturated and the rate of pollen export is unlikely to depend on the number of flowers produced (de Jong *et al.*, 1999). In general, for wind-pollinated species the

male fitness gain should increase linearly with increased investment in the reproductive function (e.g. Charnov, 1982). On the population level, increased pollen density may also promote individual female fitness, in particular when seed set depends on the availability of outcross pollen, as in self-incompatible species. For example, for the self-incompatible grass *Leymus chinensis*, seed set per flower was highest when flowers opened on days with the highest pollen density (Huang *et al.*, 2004). For wind-pollinated, mast-flowering species it has been hypothesized that during years with high flower densities the rate of fertilization, in particular by outcross pollen, is increased compared with years with low flower densities (Nilsson and Wästljung, 1987; Norton and Kelly, 1988; Smith *et al.*, 1990). Kelly *et al.* (2001) proposed that variability in the reproductive effort, in the present case pulsed flowering, would be beneficial when the mean reproductive effort results in a lower fraction of ovules pollinated than at high flowering efforts. This should be true for many outcrossing species or species suffering from pollen limitation. In contrast, self-compatible plants and species with highly efficient wind-pollination and/or with high plant densities may not benefit from such variability.

However, somewhat complicating the interpretation of the present observations, self-fertility has been described as 'very frequent and successful' in *Juncus* (Buchenau, 1890, 1892, p. 378). Selfing has been stated explicitly for some of the species studied (*J. conglomeratus, J. effusus, J. inflexus*; Graebner, 1934; Richards and Clapham, 1941; Edgar, 1964). Also, progeny array analyses using microsatellite markers revealed selfing rates of $>90\,\%$ in three natural populations of *J. atratus* (Michalski and Durka, in press). Thus, selfing seems to be common in *Juncus* species. For the *Juncus* species investigated here, this presumption is further supported by pollen to ovule ratios (P/O) per flower, which were very low when compared with other wind-pollinated taxa (P/O $<$ 386:1; S. G. Michalski and W. Durka, unpubl. res.). Given this fact, the elaborated pulsed flowering in *Juncus* would constitute an unnecessary adaptation.

However, for one of the species investigated (*J. atratus*) an analysis of the mating system (S. G. Michalski and W. Durka, unpubl. res.) revealed that despite the high selfing rates the species is effectively outcrossed due to high levels of inbreeding depression. In a microsatellite analysis of 16 populations, high levels of individual heterozygosity and low population-level inbreeding coefficients were found. This pattern is very unusual for autogamous species. Two marker-based estimates of inbreeding depression ($\delta = 1 -$ relative fitness of selfed progeny) revealed extremely high levels of inbreeding depression close to unity indicating that outcrossed progeny had much higher chances to survive than selfed progeny. Thus, due to the extensive inbreeding depression in populations of *J. atratus*, selfing seems largely irrelevant in terms of selection on flowering phenology and mechanisms enhancing outcrossing may be selected for. It remains an open question whether this pattern applies to other *Juncus* species too. A similar mechanism has been proposed for the self-fertilizing and mast-flowering species of the grass genus *Chionochloa*. It was shown that in mast years the quantity of seeds produced per flower is not any different from the one of non-mast years. However, because inbreeding depression was found to be high, it was argued that the increased quality of seeds produced through outcrossing during mast years may provide sufficiently strong selective pressure to select for masting (Tisch and Kelly, 1998).

In conclusion, the flowering in nine wind-pollinated *Juncus* species has been documented that is distinguished from other flowering patterns by distinct events of flowering pulses synchronized within and among individuals throughout a population and interrupted by days without or with few open flowers has been documented in nine wind-pollinated *Juncus* species. This results in a high day-to-day variation of flowering. It is proposed that the selective benefit of this pulsed flowering may arise by at least two facts. First, the risk of reproductive failure due to unfavourable weather conditions for wind-pollination will be reduced by spreading the flowering events across the flowering season. Secondly, high flower densities due to synchronous flowering pulses increase pollination efficiency and the rate of outcrossing. Although flowering has often been described as affected by temperature or humidity it was not possible to determine a common environmental cue for the pulsed flowering in the *Juncus* species studied.

## ACKNOWLEDGEMENTS

We like to thank Michael Burkart for providing plants of *J. atratus* and Kjell Bolmgren and anonymous reviewers for helpful comments on the manuscript. This work was financially supported by the German Research Foundation (DFG).

## LITERATURE CITED

**Ackerman JD. 2000.** Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. In: Pacini E, Dafni A, Hesse M eds. *Pollen and pollination*. Wien: Springer, 167–185.

**Adler GH, Kielpinski KA. 2000.** Reproductive phenology of a tropical canopy tree, *Spondias mombin. Biotropica* **32**: 686–692.

**Albert MJ, Escudero A, Iriondo JM. 2001.** Female reproductive success of narrow endemic *Erodium paularense* in contrasting microhabitats. *Ecology* **82**: 1734–1747.

**Allison TD. 1990.** Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. *Ecology* **71**: 516–522.

**Almeida-Neto M, Lewinsohn TM. 2004.** Small-scale spatial autocorrelation and the interpretation of relationships between phenological parameters. *Journal of Vegetation Science* **15**: 561–568.

**Augspurger CK. 1981.** Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* **62**: 775–788.

**Augspurger CK. 1983.** Phenology, flowering synchrony, and fruit set of six neotropical shrubs. *Biotropica* **15**: 257–267.

**Barrett SCH. 2002.** The evolution of plant sexual diversity. *Nature Reviews Genetics* **3**: 274–284.

**Bawa KS. 1983.** Patterns of flowering in tropical plants. In: Jones CE, Little RJ eds. *Handbook of experimental pollination biology*. New York, NY: Van Nostrand Reinhold, 394–410.

**Bertin RI, Sholes ODV. 1993.** Weather, pollination and the phenology of *Geranium maculatum*. *American Midland Naturalist* **129**: 52–66.

**Bhardwaj M, Eckert CG. 2001.** Functional analysis of synchronous dichogamy in flowering rush, *Butomus umbellatus* (Butomaceae). *American Journal of Botany* **88**: 2204–2213.

**Bianchi DE, Schwemmin DJ, Wagner JR WH. 1959.** Pollen release in the Common Ragweed (*Ambrosia artemisiifolia*). *Botanical Gazette* **120**: 235–243.

**Bianchini M, Pacini E. 1996.** Explosive anther dehiscence in *Ricinus communis* L. involves cell wall modifications and relative humidity. *International Journal of Plant Sciences* **157**: 739–745.

**Bolmgren K. 1998.** The use of synchronization measures in studies of plant reproduction phenology. *Oikos* **82**: 411–415.

**Bolmgren K, Eriksson O, Linder HP. 2003.** Contrasting flowering phenology and species richness in abiotically and biotically pollinated angiosperms. *Evolution* **57**: 2001–2011.

**Buchenau F. 1890.** Monographia Juncacearum. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **12**: 1–495.

**Buchenau F. 1892.** Ueber die Bestäubungs-Verhältnisse bei den Juncaceen. *Jahrbücher für wissenschaftliche Botanik* **24**: 363–424.

**Buide ML, Diaz-Peromingo JA, Guitian J. 2002.** Flowering phenology and female reproductive success in *Silene acutifolia* Link ex Rohrb. *Plant Ecology* **163**: 93–103.

**Charnov EL. 1982.** *The theory of sex allocation*. Princeton, NJ: Princeton University Press.

**Cox PA. 1991.** Abiotic pollination: an evolutionary escape for animal-pollinated angiosperms. *Philosophical Transactions of the Royal Society of London, Series B* **333**: 217–224.

**Culley TM, Weller SG, Sakai AK. 2002.** The evolution of wind pollination in angiosperms. *Trends in Ecology & Evolution* **17**: 361–369.

**Diekmann M. 1996.** Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. *Canadian Journal of Botany* **74**: 528–537.

**Drabkova L, Kirschner J, Vlcek C. 2006.** Phylogenetic relationships within *Luzula* DC. and *Juncus* L. (Juncaceae): a comparison of phylogenetic signals of *trn*L-*trn*F intergenic spacer, *trn*L intron and *rbc*L plastome sequence data. *Cladistics* **22**: 132–143.

**DWD. 2004.** Deutscher Wetterdienst, Agrarmeteorologischer Wochenbericht für Brandenburg, Sachsen-Anhalt, Thüringen und Sachsen, 23–33.

**Edgar E. 1964.** The leafless species of *Juncus* in New Zealand. *New Zealand Journal of Botany* **2**: 177–204.

**Eriksson O. 1995.** Asynchronous flowering reduces seed predation in the perennial forest herb *Actaea spicata*. *Acta Oecologica* **16**: 195–203.

**Faegri K, van der Pijl L. 1979.** *The principles of pollination ecology*, 3rd edn. Oxford: Pergamon Press.

**Felsenstein J. 1985.** Phylogenies and the comparative method. *American Naturalist* **125**: 1–15.

**Fenner M. 1998.** The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **1**: 78–91.

**Fenner M, Cresswell JE, Hurley RA, Baldwin T. 2002.** Relationship between capitulum size and pre-dispersal seed predation by insect larvae in common Asteraceae. *Oecologia* **130**: 72–77.

**Garland T, Harvey PH, Ives AR. 1992.** Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Botany* **41**: 18–32.

**Gentry AH. 1974.** Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* **6**: 64–68.

**Gómez GM. 1993.** Phenotypic selection on flowering synchrony in a high-mountain plant, *Hormathophylla spinosa* (Cruciferae). *Journal of Ecology* **81**: 605–613.

**Graebner P. 1934.** Juncaceae. In: Kirchner O, Loew E, Schröter C, Wangerin W eds. *Lebensgeschichte der Blütenpflanzen Mitteleuropas*, Band I, Abteilung 3. Stuttgart: Verlag für Landwirtschaft und Naturwissenschaften, 80–221.

**Harder LD. 2000.** Pollen dispersal and the floral diversity of monocotyledons. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Melbourne: CSIRO, 243–257.

**Harvey PH, Purvis A. 1991.** Comparative methods for explaining adaptations. *Nature* **351**: 619–624.

**Heinrich B. 1976.** Flowering phenologies – bog, woodland, and disturbed habitats. *Ecology* **57**: 890–899.

**Herrera CM. 1998.** Population-level estimates of interannual variability in seed production: what do they actually tell us? *Oikos* **82**: 612–616.

**Huang ZH, Zhu JM, Mu XJ, Lin JX. 2004.** Pollen dispersion, pollen viability and pistil receptivity in *Leymus chinensis*. *Annals of Botany* **93**: 295–301.

**Janzen DH. 1976.** Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* **7**: 347–391.

**de Jong TJ, Klinkhamer PGL, Rademaker MCJ. 1999.** How geitonogamous selfing affects sex allocation in hermaphrodite plants. *Journal of Evolutionary Biology* **12**: 166–176.

**Kelly D. 1994.** The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* **9**: 465–470.

**Kelly D, Hart DE, Allen RB. 2001.** Evaluating the wind pollination benefits of mast seeding. *Ecology* **82**: 117–126.

**Kirschner J, Balslev H, Clemants SE, Ertter B, Alvarez MCFC, Hämet-Ahti L, *et al*. 2002.** Juncaceae 2: *Juncus* subg. *Juncus*. *Species Plantarum: Flora of the world,* Part 7. Canberra: Australian Biological Resource Study.

**Knuth P. 1898.** *Handbuch der Blüthenbiologie*. Leipzig: Engelmann.

**Koenig WD, Kelly D, Sork VL, Duncan RP, Elkinton JS, Peltonen MS, Westfall RD. 2003.** Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* **102**: 581–591.

**Kratochwil A. 1988.** Zur Bestäubungsbiologie von *Pulsatilla vulgaris* Mill. *Flora* **181**: 261–324.

**Kudo G, Suzuki S. 2004.** Flowerig phenology of tropical-alpine dwarf trees on Mount Kinabalu, Borneo. *Journal of Tropical Ecology* **20**: 563–571.

**Lepsch-Cunha N, Mori SA. 1999.** Reproductive phenology and mating potential in a low density tree population of *Couratari multiflora* (Lecythidaceae) in central Amazonia. *Journal of Tropical Ecology* **15**: 97–121.

**Lisci M, Tanda C, Pacini E. 1994.** Pollination ecophysiology of *Mercurialis annua* L. (Euphorbiaceae), an anemophilous species flowering all year round. *Annals of Botany* **74**: 125–135.

**McIntosh ME. 2002.** Flowering phenology and reproductive output in two sister species of *Ferocactus* (Cactaceae). *Plant Ecology* **159**: 1–13.

**Mahoro S. 2002.** Individual flowering schedule, fruit set, and flower and seed predation in *Vaccinium hirtum* Thunb. (Ericaceae). *Canadian Journal of Botany* **80**: 82–92.

**Malo JE. 2002.** Modelling unimodal flowering phenology with exponential sine equations. *Functional Ecology* **16**: 413–418.

**Marquis RJ. 1988.** Phenologcal variation in the Neotropical understory shrub *Piper arieianum*: causes and consequences. *Ecology* **69**: 1552–1565.

**Marten S, Quesada M. 2001.** Phenology, sexual expression, and reproductive success of the rare neotropical palm *Geonoma epetiolata*. *Biotropica* **33**: 596–605.

**Matsui T, Omasa K, Horie T. 1999.** Mechanism of anther dehiscence in rice (*Oryza sativa* L.). *Annals of Botany* **84**: 501–506.

**Melampy MN, Hayworth AM. 1980.** Seed production and pollen vectors in several nectar-less plants. *Evolution* **34**: 1144–1154.

**Murali KS, Sukumar R. 1994.** Reproductive phenology of a tropical dry forest in Mudumalai, southern India. *Journal of Ecology* **82**: 759–767.

**Murza GL, Davis AR. 2005.** Flowering phenology and reproductive biology of *Drosera anglica* (Droseraceae). *Botanical Journal of the Linnean Society* **147**: 417–426.

**Nilsson SG, Wästljung U. 1987.** Seed predation and cross-pollination in mast-seeding beech (*Fagus sylavatica*) patches. *Ecology* **68**: 260–265.

**Norton DA, Kelly D. 1988.** Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology* **2**: 399–408.

**Oliveira PE, Gibbs PE, Bianchi M. 1991.** Pollination and breeding system of *Vellozia squamata* (Liliales, Velloziaceae) – a species of the Brazilian Cerrados. *Botanica Acta* **104**: 392–398.

**Ollerton J, Lack A. 1998.** Relationships between flowering phenology, plant size and reproductive success in *Lotus corniculatus* (Fabaceae). *Plant Ecology* **139**: 35–47.

**Opler PA, Gordon WF, Baker HG. 1976.** Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography* **3**: 231–236.

**Pickering CC. 1995.** Variation in flowering parameters within and among five species of Australian alpine *Ranunculus*. *Australian Journal of Botany* **43**: 103–112.

**Pico FX, Retana J. 2000.** Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb. *Oikos* **89**: 485–492.

**Pohl F. 1929.** Beziehungen zwischen Pollenbeschaffenheit, Bestäubungsart und Fruchtknotenbau. *Beihefte des Botanischen Centralblatts* **46**: 247–285.

**Primack RB. 1980.** Variation in the phenology of natural populations of montane shrubs in New Zealand. *Journal of Ecology* **68**: 849–862.

**Primack RB. 1985.** Patterns of flowering phenology on communities, populations, individuals, and single flowers. In: White J, ed. *The population structure of vegetation*. Dordrecht: Dr W. Junk Puplishers, 571–593.

**Proença CEB, Gibbs PE. 1994.** Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytologist* **126**: 343–354.

**Purvis A, Rambaut A. 1995.** Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences* **11**: 247–251.

**R Development Core Team**. **2006.** R: a language and environment for statistical computing. http://www.R-project.org. Vienna: R Foundation for Statistical Computing.

**Rabinowitz D, Rapp JK, Sork VL, Rathke B, Reese GA, Weaver JC. 1981.** Phenological properties of wind- and insect-pollinated prairie plants. *Ecology* **62**: 49–56.

**Randall MGM. 1986.** The predation of predispersed *Juncus squarrosus* seeds by *Coleophora alticolella* (Lepidoptera) larvae over a range of altitudes in northern England. *Oecologia* **69**: 460–465.

**Rathke B, Lacey EP. 1985.** Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**: 179–214.

**Regal PJ. 1982.** Pollination by wind and animals: ecology of gegraphic patterns. *Annual Review of Ecology and Systematics* **13**: 497–524.

**Richards MB, Clapham AR. 1941.** Biological flora of the British Isles – *Juncus conglomeratus* L. (*J. communis* × *conglomeratus* E. Mey.; *J. leersii* Marsson). *Journal of Ecology* **29**: 381–384.

**Rothmaler W. 2002.** *Exkursionsflora von Deutschland*, 9 edn. Berlin: Spektrum Verlag.

**SanMartin-Gajardo I, Morellato PC. 2003.** Inter and intraspecific variation on reproductive phenology of the Brazilian Atlantic forest Rubiaceae: ecology and phylogenetic constraints. *International Journal of Tropical Biology and Conservation* **51**: 691–698.

**Schauber EM, Kelly D, Turchin P, Simon C, Lee WG, Allen RB, *et al*. 2002.** Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* **83**: 1214–1225.

**Sharma CM, Khanduri VP, Chamoli N. 1998.** The influence of air temperature and humidity on the anthesis and anther dehiscence of *Pinus roxburghii* at three different altitudes. *Current Science* **75**: 761–763.

**Silberbauer-Gottsberger I. 2001.** A hectare of Cerrado. II. Flowering and fruiting of thick-stemmed woody species. *Phyton – Annales Rei Botanicae* **41**: 129–158.

**Silvertown JW. 1980.** The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* **14**: 235–250.

**Smith CC, Hamrick JL, Kramer CL. 1990.** The advantage of mast years for wind pollination. *The American Naturalist* **136**: 154–166.

**Sola AJ, Ehrlen J. 2007.** Vegetative phenology constrains the onset of flowering in the perennial herb *Lathyrus vernus*. *Journal of Ecology* **95**: 208–216.

**Sprengel CK. 1793.** *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen*. Berlin: F. Vieweg der Ältere.

**Thomson JD. 1980.** Skewed flowering distributions and pollinator attraction. *Ecology* **61**: 572–579.

**Tisch PA, Kelly D. 1998.** Can wind pollination provide a selective benefit to mast seeding in *Chionochloa macra* (Poaceae) at Mt Hutt, New Zealand. *New Zealand Journal of Botany* **36**: 637–643.

**Torezan-Silingardi HM, de Oliveira PEAM. 2004.** Phenology and reproductive ecology of *Myrcia rostrata* and *M. tomentosa* (Myrtaceae) in Central Brazil. *Phyton – Annales Rei Botanicae* **44**: 23–43.

**Whitehead DR. 1969.** Wind pollination in angiosperms: evolutionary and environmental considerations. *Evolution* **23**: 28–35.

**Whitehead DR. 1983.** Wind pollination: some ecological and evolutionary perspectives. In: Real L, ed. *Pollination biology*. Orlando, FL: Academic Press, 97–108.

**Wilbur HM, Rudolf VHW. 2006.** Life-history evolution in uncertain environments: bet hedging in time. *American Naturalist* **168**: 398–411.

**Yoshimura J, Clark CW. 1991.** Individual adaptations in stochastic environments. *Evolutionary Ecology* **5**: 173–192.