Plant phenological research enhances ecological restoration

Elise Buisson1,2, Swanni T. Alvarado3,4, Soizig Le Stradic4,5, Leonor Patricia C. Morellato5

While phenology data (the timing of recurring biological events) has been used to explain and predict patterns related to global change, and to address applied environmental issues, it has not been clearly identified as pertinent for restoration. This opinion article thus aims to raise awareness of the potential of phenology to enhance the quality of restoration projects and ecological restoration theory. We based our analysis on a systematic literature survey carried out in February 2014, searching the words “phenology” or “phenological” in books dealing with restoration, the term “phenolog*” in the journal *Restoration Ecology*, and the terms “restoration” and “phenolog*” in the database Web of Science until February 2014. We finally selected 149 studies relevant to our goals, and first classified them according to the context in which phenology was addressed. We then analyzed them within the framework of the five key steps of restoration projects: (1) the reference ecosystem; (2) biotic resources; (3) restoration methods; (4) monitoring; and (5) adaptive management. The literature survey showed that phenological information improved decision-making in the few restoration projects in which it was incorporated. We thus advocate taking phenological data into account at all stages of restoration when appropriate: from the acquisition of baseline data on the reference ecosystem to treatment design, and from restoration action planning and timing to monitoring. Phenological data should at minimum be collected for sown, keystone, dominant, and/or rare species to improve restoration quality. Phenology studies and monitoring should be promoted in future restoration guidelines.

Key words: exotic species, genetic provenance, germination, monitoring, phenology, restoration management, seed harvest, seed mixes, seed production, species interactions

Implications for Practice

- Phenology is an integrative environmental science which should be incorporated in ecological restoration project guidelines. Concurrently, restoration can provide new insights into phenological drivers and patterns.
- Restoration often requires the use of plants, and phenological data helps identify which species is most suitable and when and where locally adapted seeds can be acquired.
- Phenological information helps select species with important ecosystem functions (e.g. early germination and establishment to reduce soil erosion), and helps improve the fine-tuning of postrestoration management regimes (e.g. fire, grazing, mowing intensity/frequency, control of invasive species).
- Phenological information (timing of flowering, seed set, nesting, etc.) improves the timing of restoration implementation.
- Phenology monitoring provides suitable indicators to assess restoration success.

Introduction

Phenology is the study of the timing of recurring biological events, the causes of their occurrence with regard to biotic and abiotic forces, and interactions among phases of the same or different species (Lieth 1974; Schwartz 2013). Phenological changes are easily monitored and have marked effects on health, biodiversity, nutrient cycling, forestry, agriculture, and the economy (Schwartz 2013; Morellato et al. 2016). The study of phenology has gained importance over the past 20 years with the increased concern over climate change (Chambers et al. 2013). Phenology data is increasingly being used to explain and predict various patterns related to other forms of global change (Schwartz 2013), as well as to address applied environmental issues (Morisette et al. 2009; Morellato et al. 2016).

Author contributions: EB, LPCM designed the study; EB, STA, SLS, LPCM targeted the research question; EB performed the review and wrote the manuscript; EB, STA, SLS, LPCM contributed to writing and revising the manuscript; EB, LPCM found the funding to carry out the study.

1Institut Méditerranéen de Biodiversité et d’Ecologie (IMBE), Université d’Avignon et des Pays de Vaucluse, CNRS, IRD, Aix Marseille Université, IUT d’Avignon, Agroparc BP 61207, 84911, Avignon cedex 9, France
2Address correspondence to E. Buisson, email elise.buisson@univ-avignon.fr
3Departamento de Geografia, Ecosystem Dynamics Observatory, Instituto de Geociências e Ciências Exatas, UNESP - Univ Estadual Paulista, Caixa Postal 178, Avenida 24A, 1515, Rio Claro, SP 13506-900, Brazil
4Departamento de Botânica, Phenology Laboratory, Instituto de Biociências, UNESP - Univ Estadual Paulista, Avenida 24A, 1515, Rio Claro, SP 13506-900, Brazil
5Biodiversity and Landscape Unit, Gembloux Agro-Bio Tech, University of Liege, Passage des Déportés 2, 5030, Gembloux, Belgium

© 2016 Society for Ecological Restoration
doi: 10.1111/rec.12471
Supporting information at:
While phenology is an interdisciplinary science that has contributed to many disciplines, so far it has not been clearly identified as pertinent for restoration. Morellato et al. (2016) have recently highlighted the importance of phenology for conservation science and management, pointing out the likely implications of phenology for restoration ecology, particularly for seed collection. However, their paper does not explore the various situations in which phenological research can potentially improve the quality of ecological restoration projects. We thus provide here a discussion of how phenological research should be incorporated in ecological restoration. We base this opinion article on a literature survey in which we examined 149 books, book chapters, or papers relating phenology and restoration (Appendices S1 & S2, Fig. S1, Tables S1–S3, Supporting Information). Most studies dealt with plant phenology and restoration, likely because plant material is the most important biotic resource used to restore ecosystems. We examine these studies within the framework of the five key steps of restoration projects (Fig. 1): (1) establish the reference ecosystem; (2) identify biotic resource needs and sources, and obtain them; (3) implement selected restoration methods and strategies; (4) set up permanent monitoring; and (5) implement adaptive management procedures (Clewell et al. 2005). We lastly discuss how restoration ecology can also contribute to phenological research by providing new insights that will help explore innovative questions on drivers and patterns in phenology.

How Can Phenology Improve Baseline Data on Reference Ecosystems and Biotic Resources for Restoration?

Ecological restoration often requires modification of the physical environment and vegetation manipulation (Whisenant 1999), with the fauna frequently expected to colonize by itself. Although more attention is paid to the animal component nowadays (e.g. taking species interactions into account, or avoiding disturbance to the fauna), the biotic resources used in restoration projects often remain plant material. Despite the fact that animal phenology can be a key factor in improving pollination, seed dispersion, and invasive species control (Morellato et al. 2016), and that animals’ presence is likely an indicator of restoration success, our review showed that less than 10% of studies refer to animal phenology (and around 15% look at interactions of plants with animals, mainly pollinators, or herbivores). The following sections therefore focus more on plant communities and specify the reasons why it is important to collect detailed information on the phenology of plant communities of the reference ecosystem and of the restored site (Fig. 1).

Gathering Local Plant Material

Local biotic resources are best for carrying out restoration (Bucharova et al. 2016) and can be obtained by gathering local
Phenology and restoration ecology

Optimizing Seed Production

Prior to seed harvest, management of reference sites can be adapted to optimize seed production, which requires a good understanding of specific management effects on plant phenology. Some of the papers we reviewed investigated fruit production under different management strategies, such as increased soil fertility and decreased toxicity. For example, González Melo and Parrado Rosselli (2010) show that the Andean oak (Quercus humboldtii) yields more fruit on soils with a high content of phosphorus and potassium and low soil aluminum. They thus suggest managing the soil to optimize fruit production. Other articles address flowering, fruit production, and seed set in relation to disturbance intensity or frequency (fire, grazing, mowing, etc.). Meyer and Schiffman (1999) demonstrate that fire season is a significant factor in grassland restoration, and that the impact of different fire seasons on restoration success is determined by plant phenology patterns and season-specific fire intensities. Wrobleski and Kauffman (2003) indicate that prescribed fire can increase native flower abundances, providing more seeds to be collected for restoration projects. When appropriate, we thus suggest the use of prescribed fires as a management tool to improve fruit production (Figs. 2 & S2).

Producing Local Plant Material

Gathering wild local plant material is not always an option for restoration: (1) because the reference ecosystem may either be protected, ruling out seed harvest, or no longer exist; (2) because the area to be restored may be too big compared to the areas of remaining reference ecosystem; or (3) because it is not very efficient compared to the commercial production of seeds of local provenances. The latter technique is often used,
and here too phenology studies can help solve problems of propagation for species yielding low quantities of viable seeds (e.g. *Spartina alterniflora*, salt marsh cordgrass; Fang et al. 2004). The proportion of each species in commercial seed mixes is determined using various functional types, and early phenology can be a useful criterion to take into account (Carter & Blair 2012). During propagation, the timing of germination, flowering, and fruiting of wild plants can change over several generations, because phenological traits are under strong selection. Thus, the plant material might become phenologically ill-adapted (Schröder & Prasse 2013). Additionally, once on the restoration sites, cultivated plants can be naturally selected, thus favoring a particular trait, e.g. earlier flowering phenology (Kulpa & Leger 2013). Considering these phenological issues ahead of seeding and out-planting, and even ahead of production, can reveal the importance of using locally adapted plant material (Kiehl et al. 2014) to enhance plant establishment and to increase functional diversity and ecosystem functioning, thus improving restoration.

**Conserving Genetic Diversity and Local Adaptations**

Phenological studies can help address the issues related to seed collection by: (1) preventing the reduction of genetic diversity of local ecotypes (Holmstrom et al. 2010); and (2) ensuring that seeds are phenotypically suited to their home conditions (Miller et al. 2011). Phenological studies that examine whether flowering times overlap can determine whether native but non-local genotypes introduced on restored sites have the potential to cross-pollinate and to hybridize with surrounding remaining natural genotypes (Holmstrom et al. 2010). Indeed, some introduced genotypes can have advantages over local plants in vegetative and/or sexual reproduction, and can out-compete native genotypes or colonize outside of restoration sites (Holmstrom et al. 2010). Detection of this advantage is particularly important in the case of small and isolated populations (Holmstrom et al. 2010). Information on the dates of budbreak, germination, flowering and/or seed set, and on flower abundance (Miller et al. 2011) have proven essential to guarantee that using locally adapted seed sources preserves adequate phenological cycles and to ensure the reproductive success of introduced species.

**Taking Species Interactions and Ecosystem Services Into Account**

Because leaf, flower, and fruit phenologies link plants to herbivores, pollinators, frugivores, and seed dispersers, studying plant phenology involves taking into account resource availability and interaction networks, encompassing ecosystem and landscape complexity (Hagen et al. 2012). In the context of food webs, phenology helps detect when and in which conditions a particular food resource is available, and can pinpoint habitat restoration needs for the species feeding on this particular resource (e.g. Wroblewski & Kauffmann 2003). When restoring/reintroducing a population, some knowledge of species phenology (food, competitors, etc.) regarding this restored population is particularly important. As an example, phenology can provide restorationists with a method that selects plant species based on the timing of fruiting. This will enable them to attract potential seed dispersers and provide fruits all year long (Garcia et al. 2014), to match fruit availability with frugivore requirements over time and space (Gosper & Vivian-Smith 2009), and to connect the landscape through resources for both pollinators and seed dispersers (Hagen et al. 2012; Morellato et al. 2016). Phenology thus facilitates the restoration of ecosystem services, such as key food and other nontimber resources (e.g. fruits, leaves, medicinal plants), and can help sustain human population needs (Garibaldi et al. 2013) (see another example in Appendix S2 and Fig. S2). Plant phenology on restoration sites should be combined with the phenology of pollinators, seed dispersers, or migrating species among others (Schellhorn et al. 2015). This would make it possible to encompass not only most scales (from local communities to ecosystems, focusing on connectivity across the landscape) but also time (e.g. asynchrony on flowering or fruiting time between restored and reference sites may break the temporal connectivity between vegetation patches).

**How Can Phenology Enhance Restoration Treatments and Management?**

**Optimizing the Timing of Restoration Treatments**

Restoration treatments also have to be finely tuned and timed to maximize target species establishment and minimize the harm done to healthy populations of plants or animals remaining in the degraded site to be restored. To achieve this, the phenology of different groups of species (not just plants) needs to be known. Phenological information can be useful to avoid disturbance (e.g. destruction of bird nesting) during the restoration process or to maximize plant establishment from the seed bank. A calendar taking into account the phenology of both animals and plants is often the basis of restoration planning (Jaumatre et al. 2011), although it is rarely clearly stated as phenological information in the papers reviewed.

**Dealing With Exotic Species**

In the case of restoration involving removal or control of exotic species, appropriate timing of treatment application requires knowledge of both native and exotic species phenology. Exotics can leaf or bloom during times when natives do not (thus filling a vacant niche), or can flower or germinate earlier than natives (thus benefiting from a priority effect; Wolkovich & Cleland 2011; Fig. 1). Restoration treatments should therefore be applied when exotics are vulnerable but natives are not (e.g. fire, grazing, herbicide; Marushia et al. 2010; Ruckman et al. 2012).

Phenology studies can also facilitate accurate identification of the risks from non-native species. For example, precise identification of natives and exotics with matching phenology may pinpoint species that could then hybridize and induce a loss of both genetic diversity and locally adapted populations (Vilà et al. 2000). Species with matching phenologies can also be in
competition for pollinators and dispersers, thereby altering fruit quantity, quality, and dispersal, and thus community structure and ecosystem functioning (Vilà et al. 2000; Morellato et al. 2016).

Recovering Ecosystem Functions
Because of the constant feedback occurring between the abiotic environment and the biota (Temperton et al. 2004), precise information on the phenology of species can allow restorationists to reintroduce species that contribute to the recovery of some ecosystem functions. Native species with spring phenologies can reduce early-season nutrient runoff (Brudvig 2010). Fire can increase flower abundance and extend phenology, which can have a positive effect on bird species foraging activities (Wroblewski & Kauffman 2003) (Fig. 2). Therefore, taking phenology into account when planning the timing and intensity of restoration treatments will enhance restoration of ecosystem regulating functions (e.g. nutrient conservation) or supporting functions (e.g. food resources). Moreover, enriching plant communities invaded by exotic species with selected native species of matching phenologies and competitive characteristics can help them out-compete undesired species (Simmons 2005). Finally, phenology is an essential parameter to evaluate restoration treatments and postrestoration management (e.g. Carter & Blair 2012). This should encourage restorationists: (1) to focus on ecosystem functions and species composition not only as goals but also as tools to reach restoration objectives (Shackelford et al. 2013) and (2) to incorporate phenology in restoration planning (Fig. 1).

How Can Phenology Improve Restoration Monitoring?
Monitoring sites before and after restoration is essential in order to assess the success of restoration projects in achieving predefined goals and to improve future restoration practices (Holl & Cairns 2002). It is also one of the main aspects that need improvement in restoration projects (Palmer et al. 2005). Parameters monitored for restoration depend on the objectives of the project and can be very diverse (Kollmann et al. 2016), ranging from ecosystem functioning to the presence of target species such as plankton (Anneville et al. 2007) or aquatic plants (Cho & Poirrier 2005), reference grassland species (Kiehl et al. 2006), forb species (Wroblewski & Kauffman 2003), trees (Garcia et al. 2014), larval amphibians and predatory macroinvertebrate families (Curtis & Paton 2010), and seabirds (Hall & Kress 2004).

The main phenological monitoring techniques are based on seasonal in-the-field species monitoring, but recent studies have used remote sensing to monitor restored ecosystems: Dufour et al. (2013) applied Light Detection And Ranging (LiDAR), radar, and Unmanned Aerial Vehicle (UAV), and van Leeuwen (2008) analyzed a Normalized Difference Vegetation Index (NDVI) from satellite imagery. Repeated photographs taken by digital cameras can also be a cheap and efficient way to monitor species and community changes over time (see Richardson et al. 2009; Alberton et al. 2014), before or after restoration.

What Can Phenology Research Learn From Restoration?
The different phenological studies included in restoration projects were carried out with various restoration improvement aims: identify the best plan monitoring time (Cho & Poirrier 2005), define the right timing for application of restoration treatments (Cho & Poirrier 2005), study the effects of restoration treatments on interactions (Wroblewski & Kauffman 2003; Anneville et al. 2007; Garcia et al. 2014), provide information on the effectiveness of restoration treatments (Kiehl et al. 2006) and plan management (Curtis & Paton 2010). However, well-established monitoring in restoration ecology can also feed long-term phenological databases on reference ecosystems, target, dominant, or rare species, providing many new insights into phenological patterns (Table 1). A wide range of research questions remains to be tackled (Table 1). Can the phenology of native species or invasive species determine their co-occurrence or their ability to colonize and become established in the restored area? Do we observe variations in phenological patterns in plant species/decomunities that could be related to the modification of edaphic conditions? Can we reestablish interactions or ecosystem services using nonlocal plants or using local plants according to their phenology? Do some restoration treatments affect plant phenology, and how do these treatments affect plant–animal interactions? As restoration is commonly seen as an acid test of theoretical ecology (Bradshaw 1990), we suggest that restoration can enhance the understanding of phenological patterns within the framework of land use change.

Conclusion
This article aimed to increase awareness of the potential of phenological research to improve the quality of ecological restoration projects. While our literature survey demonstrates this potential, we find that phenology is currently mainly applied to assessing biotic resources. Thus, we conclude that phenology remains widely underexplored within restoration projects. Yet phenology has a huge capacity to improve the quality of ecological restoration, and many more applications to restoration remain to be explored.

In order to better understand the role that phenological research can play in restoration, restorationists and land managers should: (1) acknowledge that they are using phenological data (phenological data is often used empirically without being mentioned in technical reports and articles); and (2) work at incorporating phenology into all stages of restoration projects, when appropriate. Restoration guidelines should promote at least basic, rapidly performed phenology monitoring tasks, such as regular monitoring of sown, keystone, dominant or rare species on restored sites. The Society for Ecological Restoration International Science & Policy Working Groups should promote the use of phenology in restoration projects in appropriate documents, such as future restoration guidelines (e.g. Shackelford et al. 2013).
Table 1. Research questions and items that can be tackled on phenology (right-hand side) within the context of restoration projects. We organized them according to the five major key steps of restoration projects (Clewell et al. 2005; left-hand side).

<table>
<thead>
<tr>
<th>Key Steps of Restoration Projects</th>
<th>Phenology Research Questions</th>
</tr>
</thead>
</table>
| (1) Establish the reference       | Phenological data collected to set up restoration projects can generate a good database useful for phenological studies at broad scales. Data can be collected both on the reference ecosystem (e.g. calendar for seed collection) and on the species that established after disturbance on the area to be restored.  
  • Can phenology help us to understand the occurrence of species and/or their ability to colonize and establish in degraded areas?  
  • Do we observe changes in the phenology of species occurring in restored/degraded areas, in comparison to the phenology observed in pristine areas (phenological differences linked to different environmental conditions, such as microclimate or soil conditions)? |
| (2) Obtain biotic resources       | Phenological data collected to improve seed collection, to produce seedlings, and to better select species, and results of restoration projects using local and nonlocal plant species, can bring new insight on local phenological patterns.  
  • Are there advantages in using nonlocal versus local plants depending on their phenology?  
  • Are there phenological differences between invasive species and native species or between commercially produced populations and local populations on restored areas? This can e.g. bring new insight on invasive species success. |
| (3) Implement the selected restoration methods | Phenological data collected on restored areas and on the species established after restoration. To explore particular questions on the effects of soils or succession on phenology, one can use restored areas instead of having to build specific large-scale protocols.  
  • Does the restoration treatment (nutrient application, mowing, fire, etc.) affect plant phenology? This should help to understand the impact of nutrient increase on plant phenology. Does mowing applied to restore plant communities modify plant phenology? How does this affect plant–animal interactions?  
  • How do restoration actions influence plant phenology and plant–animal interactions, such as pollination and seed dispersal?  
  • Do the control of invasive species as a treatment to restore degraded areas impact the phenology of invasive species (e.g. fruit production) and/or of native species (e.g. changes of quantity of pollinators might alter phenology or seed production of native species transplanted/translocated in degraded areas)? |
| (4) Set up permanent monitoring  | Phenological surveys might be one ecosystem variable that can be used in a restoration evaluation, and phenological data collected during restoration monitoring may generate a good database and long-term datasets useful for phenological studies.  
  • Monitoring the restored communities should be carried out along with monitoring reference communities which serves as controls; long-term datasets can thus be collected on reference areas and contribute to answering questions such as how is climate change influencing plant phenology in both restored and pristine areas?  
  • With phenological data on the restored area: How does plant community phenology change along succession? Does restoring plant communities lead to the recovery of plant–animal interactions?  
  • Assessment of the phenology of some transplanted species can improve the global understanding of such species  
  • New techniques of phenology monitoring can be applied to ecological restoration (i.e., monitoring restored communities) and bring some feedback on these techniques as well as the plant responses over time  
  • Monitoring phenology of restored communities improves our understanding of the ecology of the pristine communities including the plant–animal interactions and their importance to the structure and resilience of plant and animal communities. |
| (5) Implement adaptive management | Adaptive management on restored sites may generate data coupled with particular management regime.  
  • How does plant phenology change with changes in management type or regime?  
  • How do finely timed plant–animal interactions change with restoration?  
  • Can restored phenological patterns help reestablish interactions or ecosystem services and with what management regime? |

Acknowledgments

The authors would like to thank Megan F. King and Marjorie Sweetko for reviewing the English, and the Phenology Lab members, F. Mesléard, T. Dutoit, two reviewers and coordinating editor S. Allison for improving previous versions. This work was supported by: EB—French Embassy/UNESP Rio Claro Chairs 2012 and 2014; March 2017 Restoration Ecology 169
LITERATURE CITED


van Leeuwen V (2008) Monitoring the effects of forest restoration treatments on post-fire vegetation recovery with MODIS multitemporal data. Sensors 8:207–2042


Schröder R, Prasse R (2013) From nursery into nature: a study on perfor-
Phenology and restoration ecology


Simmons MT (2005) Bullying the bullies: the selective control of an exotic, invasive annual (Rapistrum rugosum) by oversowing with a competitive native species (Gaillardia pulchella). Restoration Ecology 13:609–615


Coordinating Editor: Stuart Allison


Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Literature survey and reviewing process.

Table S1. Title, year of publication and authors or editors of the 42 books dealing with restoration that were searched for the word “phenology” or “phenological.”

Table S2. Categories adopted to classify the studies used in the literature review according to the different contexts in which phenology and restoration were addressed in the studies.

Appendix S2. Results of the survey.

Table S3. List of the 149 relevant chapters or papers selected for this study.

Figure S1. Flow chart detailing the process of paper collection and elimination for the study.

Figure S2. Example of application of phenology to restoration based on a study by Alvarado et al. (2014) carried out with the following reference ecosystem: Uapaca bojeri (tapia) woodlands, Highlands of Madagascar.

Received: 28 March, 2016; First decision: 26 April, 2016; Revised: 19 October, 2016; Accepted: 28 October, 2016; First published online: 9 December, 2016