

## Bradychory – The coining of a new term

C.A. Thanos

*Department of Botany, Faculty of Biology, University of Athens, 15784 Athens, Greece*  
*cthanos@biol.uoa.gr*

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ABSTRACT: A newly coined term, bradychory, is put forward. Bradychory (literally meaning ‘slow dispersal’) is defined as ‘delayed dispersal’ and is suggested to fully replace bradyspory, a seldom used term. Bradychory is also suggested to replace serotiny in all the uses of the latter in the field of dispersal. On the other hand, serotiny is proposed to denote only the structural aspect of reproductive units that remain closed at maturity (thus retaining their seeds enclosed for months or years and eventually leading to the accumulation of a canopy - aerial - seed bank). Bradychory is wider as a term than serotiny (at its current use) and encompasses all cases of delayed dispersal: closed cones or fruits as well as all additional instances of seasonal delay of seed dissemination. Bradychory is common not only in the well-known cases of fire-prone ecosystems but also in seasonally dried environments, such as deserts and Mediterranean-type habitats. Bradychory is viewed as a mode of dispersal which comprises the entire group of adaptations that share the common trait of delayed dispersal; it can be distinguished further into two main subgroups: seasonal bradychory (delay of a few months up to one year) and episodic bradychory (one to many years). The underlying mechanisms of seed retention on the mother plant are diverse and similarly are the cues for seed liberation (fire and rain being the most important among them). The postulated advantage of bradychory is the timing of seed dispersal at conditions that maximise and optimise seedling recruitment and establishment; in this aspect, bradychory can be regarded as a strategy complementary to seed dormancy.

### 1 INTRODUCTION

#### 1.1 *Serotiny*

Serotiny as a term denoting ‘late liberation of seeds’ was used for the first time by Michaux (1803) when he named a new pine species with closed cones as *Pinus serotina* (see Le Maitre 1985, Lamont 1991, Lamont et al. 1991). *Serotinus* is a latin word meaning ‘late-occurring’ and during the last 2 centuries ‘serotiny’ and ‘serotinous’ have been quite widely used to define the closed-coneness of many pine species (and other gymnosperms; Vogl et al. 1977) while relatively recently the term was also applied to the closed-fruited angiosperms of the southern hemisphere (Bond 1985, Le Maitre 1985, Lamont 1991, Lamont et al. 1991). A query with the keywords ‘serotiny’ and ‘serotinous’ in the ISI database returned a number of about 100 papers published in peer-reviewed, international journals, during the last 25 years.

In the world flora nomenclature, *serotinus* has been used in tens of cases, always denoting 'late flowering'. In the Greek flora, in particular, there exist at least 8 taxa with *serotinus* (-a, -um) as their specific or subspecific name: *Carex serotina*, *Cleistogenes serotina*, *Cyperus serotinus*, *Limonium serotinum*, *Narcissus serotinus*, *Odontites verna* subsp. *serotina*, *Ophrys mammosa* subsp. *serotina*, *Taraxacum serotinum*. An eminent example is *Narcissus serotinus* L. which was named by Linnaeus himself on the basis of late flowering; this species was already described as late-flowering by Theophrastus (*HP* 6.6.9): 'its flowering occurs extremely late, around the autumnal equinox' (and recognised as *hysteranthus* by Negbi, 1989). Therefore, the statement that 'the term serotiny has usually been applied to delayed seed release rather than delay in other plant functions' (Lamont 1991) is only partly true.

## 1.2 *Bradyspory*

The terms bradyspory and tachyspory seem to appear for the first time in the early part of the 20<sup>th</sup> century (*A glossary of botanic terms with their derivation and accent*, Jackson 1916). However, it seems that it was Sernander (1927) who introduced these terms in the study of seed dispersal, along with several other ones (diaspore being an eminent example among them). Sernander (1927) distinguished tachysporous plants ('tachy-' from the Greek fast), where the diaspores are set free immediately after maturation and bradysporous plants ('brady-' from the Greek slow) where liberation comes only after a long delay. The delay can be one winter ('Wintersteher') or one summer, or some indefinite period (termed macrobiocarp).

Recent citations to bradyspory (and other uses of the term) include Stock et al. (1990), Meney et al. (1994), Whelan et al. (1998) and Price and Morgan (2003). Above all, Whelan (1995) discussed in detail the semantics of serotiny and bradyspory and chose (on the basis of a few previous works, such as Specht 1979) to adopt bradyspory. However, the majority of the scientific community seems to favour, by far, the use of serotiny (only 4 hits with bradyspory were returned by the ISI database).

## 2 DISCUSSION

### 2.1 *The importance of timing in dispersal*

The temporal vector of dispersal (i.e. the timing of dissemination and presentation of dispersal units) is surprisingly neglected in the all-inclusive, recent review on the ecology and evolution of seed dispersal (Levin et al. 2003). This may be the result of viewing the 'delayed dispersal' mechanisms as cases of on-plant seed storage (canopy seed banks). This is partly true but since the dispersules are still on the mother plant, from the view-point of dispersal, the latter is 'postponed' for some time in the future, after a shorter or longer period. Therefore, apart from the obvious (and most important) spatial vector of seed dispersal, there exists the time dimension as well: the dispersal dynamics (i.e. the onset and duration of dissemination in reference to seed maturation) are important parameters, which should be integrated into the spatial analysis of the phenomenon.

Keeley and Zedler (1998) in their discussion of pine life histories described serotiny as a structural trait (on the basis of the North American working definition) but eventually agreed with Lamont et al (1991) who had proposed that a broader definition of serotiny (encompassing canopy seed storage) is necessary. However, in the glossary of the same book (Richardson 1998), serotiny is defined as 'a morphological feature of some pine cones (and reproductive structures in other plants) whereby the cones remain closed and on the tree for one or more years after seed maturation: cones open rapidly when high temperatures melt the resin that seals the cones scales'.

### 2.2 *Introduction and definition of bradychory*

A new term of seed dispersal is put forward: **bradychory** from the Greek *brady-* (slow, late) and the 'official' suffix of dispersal modes *-chory*.

Bradychory, literally meaning ‘slow dispersal’ is defined as ‘delayed dispersal’ and includes closed cones and fruits as well as those structures that remain semi-open or alternating from open to closed thus retaining a portion of seeds (while a fraction only of seeds are dispersed each time).

Although it is in this work that bradychory is officially proposed for the first time, it has been in sort of ‘test-use’ for several years and in various instances. The new term made its debut in the Greek literature, a decade ago (Thanos et al. 1994) and since then it reappeared in several other works (Thanos et al. 1995, Kadis 1995, Doussi and Thanos 1999, Doussi 2000 and Skourou 2003). The first occurrence of the term bradychory in the international literature is found in Daskalakou and Thanos (1996); it also appeared later in Thanos (1999), Thanos (2000), Thanos and Daskalakou (2000), Skourou and Arianoutsou (2004).

The main reasons for the introduction of bradychory are: the confusion created by the competing, synonymous use of serotiny and bradyspory and the need for a ‘legitimate’ term denoting delayed seed dispersal. Serotiny in its initial, broad sense means ‘late-occurring’ and is both vague and has been widely used by taxonomists (as late-flowering); in addition, its working definition was restricted, until recently, to the morphological aspect of the closed reproductive structures. On the other hand, bradyspory and tachyspory (although not fully erroneous) may create a lot of confusion by themselves. In his introductory discourse on the ‘general terminology’ of dispersal, van der Pijl (1972) concludes with objecting the use of the suffix *-spory*. Bradyspory is semantically based on the Greek word for dispersal (*diaspora*) and the modern Greek word for seed (*sporo-*; while the ancient Greek equivalent is *sperma-*). However, the use of *sporo-* and *-spory* are obviously confusing (particularly in regard with various terms referring to haploid spores, such as megaspore, microspore, isospory, heterospory etc) and it is suggested that all their uses be abolished. Even the term diaspore (also introduced by Sernander 1927) is confusing and might be abandoned as well in favour of ‘dispersule’ or ‘unit of dispersal’.

It is well known that the established, dispersal terminology recognises 4 main classes of dispersal types (anemochory, hydrochory, zoochory, autochory) and several subclasses thereof, all termed with a prefix denoting the dispersing agent and the suffix *-chory* (van der Pijl 1972). Since *brady-* is not a dispersal agent, the legitimacy of the term bradychory could be questioned. However, in addition to the 4 main classes, there also exist a number of additional, more or less accepted terms, such as telechory, atelechory, antitelechory, achory, (topochory), diplochory, polychory which do not follow the basic rule. If these terms are accepted why not bradychory as well? In particular, the first 5 terms of the series above refer to distance of dispersal while bradychory refers to the timing of dispersal. Therefore, we consider it reasonable to accept any term related to dispersal as long as it ends in *-chory*, even if the prefix does not denote an agent of dispersal, as in the case of bradychory.

### 2.3 The occurrence of bradychory in seasonal environments

Bellairs and Bell (1990) found that decreased rainfall in a climatic gradient was a significant factor in determining the proportion of species with serotiny. Gutterman (1993) described synaptospermy in annuals and perennials where seeds are enclosed in woody fruit or capitula as in *Asteriscus pygmaeus* or in capsules as in *Blepharis* spp. (Gutterman 1972) and other species (e.g. geophytes inhabiting the Negev Desert; Kamenetsky and Gutterman 1994). The seeds remain on the dead (or aerial, dried part) of the mother plant and this phenomenon, besides to the Negev, also occurs in other deserts of western Asia and Africa; Gunster (1994) reported serotinous species in the Namib desert while reference to delayed seed dispersal is made to North American desert annuals (Venable and Lawlor 1980). Baskin and Baskin (1998) conclude that species with serotiny may grow in regions with low rainfall.

Delayed dispersal is a relatively common term in the relevant literature and it is suggested to be replaced by bradychory. In this sense, bradychory encompasses not only the ‘typical’ serotiny (encountered in many pines, Proteaceae etc) but also all those cases that refer to a seasonal delay of seed liberation and dispersal. In the former, seeds are dispersed from the mother plant after an unforeseeable event (e.g. fire or an exceptionally hot spell) that may potentially take place in a span

of years or decades; in the latter, seed dispersal takes place in a rather predictable, seasonal way, within several months after seed maturation. The underlying mechanism for the former is always the xerochastic opening of the seed ‘containers’ while in the latter it can be either by xerochasy or by hydrochastic opening, when humidity is the required signal. Both xerochastic and hydrochastic reproductive structures are known to occur in periodically dry regions (van der Pijl 1972). Therefore, bradychory can be subdivided into episodic (or long-term) and seasonal (or short-term). The latter subgroup of bradychory seems to be quite common among Mediterranean plants. Kadis (1995) observed that many among the endangered plants of Cyprus flora he was studying were seasonally bradychorous: *Alyssum akamasicum*, *Ferulago cypria*, *Phlomis brevibracteata*, *P. cypria*, *Ranunculus kykkoensis*. Similarly, Skourou (2003) recorded a gradual seed liberation for *Cistus creticus* and *C. salvifolius*. Finally, Bastida and Talavera (2002) found a very extended period of seed release (8-16 months) in *Cistus ladanifer* and *C. libanotis*. They concluded that this ‘staggered’ seed release could constitute an efficient risk-reducing trait.

Both subtypes of bradychory might be observed in a single species. Seeds in pine cones may still remain inside the cones even if the initial opening has taken place – the scales may simply ‘imprison’ the seeds until full opening takes place. Also, due to wet-dry fluctuations the cones may open and close to varying degrees liberating the seeds little by little. *Pinus attenuata* (knobcone pine) closed cones open after a fire but seeds are shed over a considerable time period (Vogl et al. 1977). This may also be the case for *Pinus brutia* (Boydak 2004) where seed dispersal is reported to occur throughout the year.

Bradychory can thus be viewed as a complementary mechanism of seed dormancy that postpones seed dispersal and dispersule ‘presentation’ until field conditions optimal for seed germination, seedling emergence and seedling establishment are met (be it months or years after seed maturation).

### 3 CONCLUSIONS

It is suggested that **serotiny** is maintained in use but only *sensu stricto* (i.e. with its initial meaning), as a structural term (along the lines adopted in the glossary of the *Ecology and Biogeography of Pinus* [Richardson 1998]) denoting: ‘a morphological feature of reproductive structures (either cones in certain pine species and other gymnosperms or fruits and other structures in several angiosperms) whereby the structures remain closed, on the plant, for one or more years after seed maturation’. **Serotinous** are both the seed-retaining structures and the plant species bearing such structures. The quantification of serotiny can be realised with the use of **degree of serotiny**, defined as the percentage of either closed structures (on an individual plant, population or species level) or plants bearing closed structures (on a population or species level).

A **canopy (aerial) seed bank** is defined as the ‘on-plant store of seeds’ and is a well-established term in the field of (natural) seed storage. A canopy seed bank is obviously the immediate result of serotiny but, in addition, seeds may be accumulated on a living (or dead) plant within half-opened, half-closed structures on which the application of the term serotinous is dubious.

From the dispersal point of view, **bradychory**, the term proposed in this work, is suggested to replace bradychory. In the same context, it is also suggested that tachyspory be abandoned while the (rather common) use of diaspore be avoided in favour of the more appropriate (and less confusing) terms dispersal unit or dispersule (or less preferably disseminule). **Bradychory** is defined as ‘delayed dispersal’ and encompasses all possible underlying mechanisms besides serotiny. Since dispersal usually refers to a plant species, **bradychorous** should basically be applied to a plant species as well (and only exceptionally to a type of seed-retaining structure). On the basis of the pertinent time scale, bradychory can be distinguished into **seasonal (short-term)** and **episodic (potentially long-term)** while (in a few cases) both types may coexist in a single species.

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