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Time-lags between introduction, establishment and rapid spread of introduced environmental weeds

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Abstract

Time-lags between the introductions of exotic plants, their establishment and subsequent spread are commonly observed in many species. In woody plants, major changes in a biotic (e.g. grazing, pollinator) or an abiotic (e.g. hurricane, flood, logging) factor determine the duration of time-lags and there is little published evidence to support the importance of other factors and genetic adaptations in particular. Human activities and perception (e.g. interest in and ability to detect the spread of an invasive) are also common explanations for some observed time-lags. The importance of time-lags in predicting, detecting and preventing the spread of introduced species is highlighted.

Introduction

In 1864, as a result of his extensive travels and field observations, J.D. Hooker stated that:

> "Among the most interesting phenomena connected with the distribution of plants, are those that concern the rapidity with which some species of one country will, when introduced into another, rapidly displace the aborigines and replace them."

Over the subsequent decades it became clear that this was not always the case as time-lags between the introductions of exotic plants and their spread did indeed occur. In fact it has since been realised that only a small proportion of introduced species actually spread and even fewer become weeds (Kowarik, 1995).

Although Hooker went on to state that "the inquiry appears to be perhaps the most interesting and important in all biology" the scientific community has shown little interest in this phenomena. Indeed, until relatively recently plant invasions have not been considered a global problem and have often been of little concern to biologists. Over the past 140 years few investigations of the existence and the causes of the rapid spread of introduced plant species have been published and the reasons underlying the existence of time-lags between the introduction and the rapid spread of plants have received even less attention.

Here I want to review the evidence as to how and why the populations of introduced woody plant species often remain, or appear to remain, small and localised for long periods of time before the species exhibit very rapid spread. Finally, from the available evidence, I will draw conclusions relevant to the prevention, detection and prediction of environmental weeds.

Existence and duration of time-lags

Invasive plants show two types of lag phases prior to a very rapid growth in population size (Kowarik, 1995). There may be a period between the introduction and the first spread of the species or the species exhibits a limited population growth.

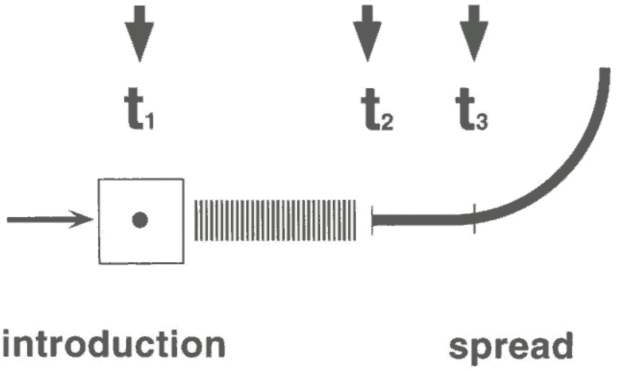

Figure 1. Two types of lag phases may be recognised: a. period between the first introduction and the first spread (t2-t1), and b. period preceding the switch to a significantly higher rate of population growth (t3-t2) (from Kowarik, 1995).

The existence of time-lags in plants has been reported in many parts of the world including Australia (e.g. Anon., 1999), Southern Africa (e.g. Hoffman, and Moran, 1988) and Northern America (e.g. Bruce, Cameron, and Harcombe, 1995). In the German province of Brandenburg Kowarik (1995) traced historical evidence of the date of introduction and that of first recorded spread. He reported that for 184 invasive species the average duration of the time-lag between the introduction and the initiation of an invasion was 131 years and 170 years for, respectively, shrubs and trees.

The time between the introduction of the species, the first record of spread and pest status of tropical invasive woody species varies, respectively, from 3 to around 50 years and 4 to around 90 years (Table 1) indicating the existence of time-lags. This is further supported by the fact that the great majority of known invasive tropical woody plant species were introduced between 1838 and 1937 with a peak in the late 19th century (Binggeli, unpublished data) but few were reported to be invasive before the second half of the 20th century. Thus the duration of time-lags is highly variable and a species may become highly invasive even when it has been introduced for a long period of time in a particular region.

Table 1. Duration (in years) of known time-lags between the introduction and first spread and pest status in tropical invasive woody plants (updated from Binggeli, Hall, and Healey, 1998).

Species	Region	Year of initial introduction	Noticed after (yrs)	Perceived as problem/pest after (yrs)
Acacia nilotica	N. Australia	1890s	c. 30	c. 60
Casuarina equisetifolia	Florida	c. 1900	c. 56	c. 65
Cecropia peltata	Ivory Coast	1920	<48	69
	Cameroon	c. 1910	c. 23	c. 36
	Zaire	1911	19	40
	Malaysia	1953	19	35
Chromolaena odorata	Ivory Coast	c. 1955	c. 7	c. 20
Cinchona succirubra	Galapagos	1946	26	40
Lantana camara	Galapagos	1938	32	40
Maesopsis eminii	East Africa	1913	14	65
Miconia calvescens	Hawaii	1961	c. 30	c. 30
	Tahiti	1937	c. 30	c. 35
Mimosa pigra	N. Australia	c. 1880	c. 36	c. 90
Psidium guajava	Galapagos	1858	?	<90
Rubus sp.	Galapagos	1983	3	4
Schinus terebinthifolius	Florida	1898	50	75

Reasons postulated for the existence of time-lags

The reasons postulated for these time-lags or lag phases are threefold (Hobbs, and Humphries, 1995):

- genotypic adaptations
- cyclical disturbance or a combination of environmental conditions
- species, with exponential growth, not observed until the population reaches a critical size.

However, until very recently little evidence was available to support these hypothetical explanations.

Factors determining time-lags

Based on published literature these three factors are reviewed in turn (unless stated all information from Binggeli, Hall, and Healey, 1998). It is worth noting that for several of the more comprehensively documented species the reasons for the observed time-lags have been inferred and only sometimes demonstrated. Indeed in the temperate zone limited evidence is available to infer the reasons for observed time-lags. Crooks, and Soulé (1997) have reviewed the evidence relating to time-lags in animals.

Genotypic adaptations

There is no published evidence indicating that time-lags in invasive woody plants result from genetic adaptations, in fact little is known about the genetic structure and differences between populations in the native and invaded ranges.

In its native range, *Rubus alceifolius* showed great genetic variability within populations and among geographically close populations (populations sampled ranging from northern Vietnam to Java). In Madagascar, where the species is invasive, genetic variability was somewhat lower whilst on other Indian Ocean islands, where it is a major weed, variation was very limited (Amsellem *et al*., 2000). In the Chinese ornamental tree, *Ailanthus altissima*, introduced to and widely planted in North America, native and introduced populations are genetically different although the amount genetic variability is the same (Feret, and Bryant, 1974). In *Rhododendron ponticum,* a widespread invader in Britain and Ireland, rDNA or cpDNA evidence of introgression from *R. catawbiense* has been found and it has been suggested that this may confers improved cold tolerance in northern Britain (Milne, and Abbott, 2000).

Although it has been argued that the differences in genetic variations between native and invasive populations are probably the result of human selection and pattern of introduction rather than adaptation to local environmental conditions (Feret, and Bryant, 1974; Amsellem *et al*., 2000), the importance of genetic adaptations as a cause of time-lags can not be discounted especially in view of limited the data available.

Abiotic factors

A number of abiotic factors have been shown to be responsible for the existence of time-lags and include wind, flooding and deforestation. In Florida *Casuarina equisetifolia* started spreading following the disturbance caused by two hurricanes. Similarly, the spread of *Cardiospermum grandiflorum* on Rarotonga (Cook Islands) was triggered by the hurricane Sally in 1986 (Meyer, 2000). Flooding is an important contributing factor in triggering the rapid spread of some species (e.g. *Acacia nilotica* and *Mimosa pigra* in Australia). *Cecropia peltata* was introduced to south-western Ivory Coast as a shade tree in coffee plantations in 1910. By the late 1950s the species had spread by only 20km. However, following the destruction of most of the remaining forest the rate of spread increased markedly in the 1960s.

In the case of asexually reproducing species, such as a species of *Selaginella* in East Africa (Binggeli, 2000), any physical barriers, such as rivers, roads and cliffs, will prevent the spread of the plant into surrounding vegetation unless this barrier is removed or a secondary human introduction has been made. Habitat isolation of poorly-dispersed plant is another cause of time-lags, especially in the case of species solely planted in botanic gardens (e.g. *Mimosa pigra* in Australia).

Biotic factors

The introduction of pollinators, marked changes in grazing and trampling are examples of biotic factors determining the duration of time lags.

The sudden introduction of a pollinating agent is one of the main biotic factors determining some time-lags. For instance, *Ficus microcarpa* widely planted as an ornamental in Florida only became a pest about 45 years after introduction, when its natural pollinator, a fig wasp (*Parapristina verticillata*), was introduced. Similar time-lags have occurred in *Ficus* spp. in Bermuda and New Zealand, but in the latter country the pollinator arrived via natural dispersal (Gardner, and Early, 1996; Francis, and Simmons, 1998).

The spread of *Hippophae rhamnoides* on Irish sand dune systems resulted from the population crash of the rabbit (*Oryctolagus cuniculus*) following the outbreak of myxomatosis in the early 1950s (Binggeli, 1992). In Hawaii sheep grazing controlled the shrub *Ulex europaeus* but a shift in land use from sheep grazing to cattle ranching allowed the species to spread. Cattle trampling produced microsites for seedling establishment and cattle failed to graze *U. europaeus* as effectively as sheep.

Other factors probably important in determining time-lags in woody plants are the ages of first flowering as well as of mass seed productions. From the evidence currently available it would appear that in the tropics time-lags are much shorter than those observed in temperate species, although the reasons for this difference is unclear. Part of the explanation probably reflects differences in the age of first flowering which are typically between one and seven years of age in tropical species (Binggeli, Hall, and Healey, 1998) but greater in the temperate zone, varying from three to around 40 years (Schopmeyer, 1974). Furthermore many temperate species undergo a period of phase change between the ages of first and full flowering (e.g. Hackett, 1985).

Interactions

Although little evidence is presently available, one can envisage that interactions between biotic and abiotic factors do occur. Woody plant species with irregular fruiting may fail to produce any seeds during a particular important disturbance event conducive to seedling establishment. In the case of *Acacia nilotica* in Australia the observed time-lag appears to be the result of a replacement of sheep by cattle associated with a series of above average wet years (Tiver *et al*., in press).

Time-lag or marked population increase?

The introduction of pollinating agent or habitat isolation (e.g. botanic gardens) are the only documented reasons for the time-lags involving a period between the introduction and the first spread of the species. In all other instances the species exhibits a limited population growth and it is often difficult or even impossible to determine whether there is a time-lag or simply marked increased in population size. In Table 2 some examples of tropical woody plant species that exhibited marked increases in population size are given.

Table 2. Biotic and abiotic factors known to influence or determine the time-lag and marked population increase of invasive woody plants in the tropics (updated from Binggeli, Hall, and Healey, 1998).

	Time-lag	Marked population increase
ABIOTIC FACTORS		
Logging/deforestation	*Cecropia peltata*	*Maesopsis eminii*
Wind - hurricane	*Casuarina equisetifolia*	*Pittosporum undulatum*
- treefall		*Passiflora mollissima*
Flooding	*Acacia nilotica* *Mimosa pigra*	
Fire		*Chromolaena odorata* *Pinus pinaster*
Nutrient enrichment		*Schinus terebinthifolius*
Habitat isolation	*Mimosa pigra*	
BIOTIC FACTORS		
Pollinator	*Ficus microcarpa*	
Grazing	*Acacia nilotica* *Ulex europaeus*	
Disperser		*Psidium guajava*
Digging by mammals		*Clidemia hirta* *Passiflora mollissima*
Trampling by mammals	*Ulex europaeus*	

These indicate that in a number of instances the same biotic and abiotic factors induce time-lags and marked populations increases. It also appears that the intensity and the periodicity of these factors may explain the observed differences. A number of other biotic and abiotic factors (including drought, frost, human-induced disturbance, hybridization and diseases) may also affect time-lags and it is well-known that they produce marked increases in woody plant population sizes.

The human factor

With rare exceptions (e.g. *Clidemia hirta* in Madagascar; Cabanis, Chabouis, and Chabouis, 1970), the reason for the introduction of a woody plant species has been purposeful, in sharp contrast with many non-woody plants. These introduced species are all linked with human activities such as agriculture, horticulture and forestry (Binggeli, Hall, and Healey, 1998) and their spread either reflects human's patterns of activities or perception of nature. In many cases apparent time-lags are clearly related to human transportation of particular species.

Propagule pressure

Often the original introduction of a woody species was limited to one or a few individuals, but a number of subsequent introductions, usually consisting of many plants, were made for a different purpose. For instance, in Hawaii and Florida a few individuals of some tree species were planted as ornamentals and some decades later these species were either widely planted in forestry plantations or large quantities of seeds were aerially sown (Anon., 1983). Some of these species were observed to spread only following these secondary introductions.

Human perception

A number of biotic and abiotic factors have been given above to explain time-lags in woody plants, however in many instances no ecological explanation can account for the observed phenomena. Historical evidence would suggest that in many cases time-lags are an artefact of human perception rather than the result of biological phenomena.

Below I outline a number of examples and attempt to provide the reasons for the failures to perceive, understand and document the invasive process correctly. A couple of examples are also given to illustrate how coincidence and even chance may be essential in determining both the existence or lack of time-lags and their duration.

In 1992 *Lantana camara*, one of the worlds most ubiquitous tropical weeds, was thought to be becoming a serious weed on the Pacific island of Pitcairn (Waldren, Florence, and Chepstow-Lusty, 1995). Yet, in 1936 a government report clearly stated that the plant was a pest and control was required (Neill, 1938). Based on the 1995 report one could have falsely concluded that *L. camara*, probably introduced around 1900, would have had a time-lag of nearly a century before becoming a pest. The inability to perceive correctly the abundance in space and time of the plant on the island resulted from lack of field observations and a failure to trace and read the ‘grey’ literature (e.g. reports and obscure journals). Furthermore, *L. camara* is not considered by Pitcairners as a weed and is in fact thought to be a soil improver, thus they would not have been drawing outsiders' attention to it.

Up to the late 1950s *Syzygium jambos* was not generally considered to be a weed on the island of Pitcairn although some mention of its invasiveness had been made in the 1930s. In fact the tree, introduced in the late 19th century, was considered to be an essential fuelwood resource. By the 1990s *S. jambos* covered a large area of Pitcairn and the species was viewed as a major threat to the island's biodiversity because of its rapid spread into various native plant communities (e.g. Diamond, 1994). In this instance no direct mention of time-lag has ever been made, but by looking at published records one could conclude that following a small population increase the species underwent a rapid expansion from around 1960 onwards. Field observations carried out in 1997 show that this rapid spread was in fact the abandonment of an agroforestry system which consisted in a patchwork of fields with field boundaries containing *S. jambos*. The spread into semi-natural vegetation is limited and slow. Published statements relating to the invasiveness of *S. jambos* relied on casual field observations and a misunderstanding of local people's perception of the species. Pitcairners' dislike for the tree focused mainly on the spreading, shallow and dense rooting system making cultivation of gardens an arduous task and on its heavy shading, rather than on the tree's ability to spread into semi-natural vegetation as understood by scientists (Binggeli, 1999a and unpublished).

A *Selaginella* sp. was introduced to the Amani Botanic Gardens (East Usambaras, Tanzania) as a greenhouse ornamental prior to World War I. Within two decades the greenhouse was abandoned and the *Selaginella* started to spread into the surrounding vegetation but the plant remained confined to the close vicinity of the greenhouse, the area being surrounded on three sides by a river and the other by a main road. During the 1980s some plant material was moved intentionally or as a contaminant to the forest edge and started to spread into the forest. At the same site a vine, *Pyrostegia venusta*, was planted around a nearby house around 1989. It soon started to smother the house and the plant was removed and discarded at the forest edge. It has since been rapidly spreading into the forest (Binggeli, 1999b, 2000). In these two instances the existence or absence of a time-lag as well as the reasons could be clearly ascertained and checked through a combination of factors. The invaded forest area was extensively investigated in the 1987 (see Hamilton, and Bensted-Smith, 1989) and unexpectedly revisited in 1999 during a field-course by the present author. Excellent historical botanical records dating back to the early part of the 20th century were readily available and finally the information could be corroborated by other scientists and local people. Without part of this information no clear conclusion to the existence or absence of time-lag could have been drawn. This clearly indicates that a certain amount of luck is essential to fully obtain this essential information.

In Ireland *Rhododendron ponticum* is a serious problem in many oakwoods of the western part of the island and has been widely reported (e.g. Cross, 1981). It is even regularly cited in the invasive literature as a classic example. In the eastern part of the island another evergreen small tree, *Prunus laurocerasus*, invades oakwoods in a similar fashion and appears to have the same impact, however this species is generally not perceived to be a problem and has gained little attention. Here, there is indeed a serious perception problem which may stem from the fact that *R. ponticum* spreads into forests with a higher conservation value containing one rare species.

In Tahiti, the spread of *Miconia calvescens* was not noticed until 30 years after its introduction, however by that stage the species was already widespread. This would suggest that in the Society Islands the observed time-lag is not an ecological phenomena but, rather, a human perception problem. That is the vegetation was little investigated and no monitoring was carried out. In Hawaii the tree was detected only following warnings emanating from French Polynesia as to the threat posed by the species. At first the tree was thought to be rather limited in extent and its eradication possible, but further systematic searches in remote areas soon uncovered large infestations (Conant, Medeiros, and Loope, 1997).

Reasons behind human perception failures and successes

From the above examples linking human perception and the detection of time-lags one can summarize the failures and successes as follows:

Failures:
- poor natural history skills and inability to understand species autecology in relation to ecosystem dynamics.
- lack of historical research and of the ‘grey’ literature in particular.
- poor use of local knowledge. Either this knowledge is not used or scientists misunderstand what locals are saying.

Successes:
- good knowledge of the local ecosystem and of the flora in particular.
- regular monitoring.
- good historical records.
- learning from experiences in other regions.
- chance.

Still, in many instances the existence of a time-lag, its duration as well as the cause(s) of its existence can not be determined despite thorough investigations, but at least the likelihood to draw the wrong conclusions will be significantly decreased.

Implications for prediction, detection and management

It is probable that most short time-lags (i.e. <10-15 years) in woody plants are caused by a lack of seed production resulting from the juvenile state of the plants. In areas where monitoring is not regular short time-lags will be an artefact of poor recording. Longer time-lags are essentially the result of secondary introductions to suitable habitats and major, and often dramatic, changes biotic and abiotic factors. Whenever an introduced species requires a particular form and/or intensity of disturbance (occurring at irregular intervals) or animal interaction (temporally absent) the duration of the time-lag may vary greatly. In woody plants there is no published evidence to suggest that some time-lags result from genetic adaptations, although in aquatic weeds evidence for strong selective pressures during colonisation exist (Barrett, 1992), and all reported instances show that major changes in biotic and abiotic factors determine the duration of time-lags. Climate change and associated changes in disturbance pattern may also facilitate the spread of species hitherto present, but not spreading, into natural and disturbed vegetation.

In relation to detection and prevention is important to learn about past disturbance regimes, both in terms of their periodicity and intensity. It is suggested that contingency plans must be made so that when an unusual abiotic (hurricane, major flood, drought, etc...) event occurs or a new species of herbivore becomes dominant, a systematic programme of field observations is carried out to detect the spread of hitherto insignificant environmental weeds.

We need to know more about the autecology of introduced species and especially phase change and fruiting periodicity. To-date most invasive woody plants may be described as early successional or specialized species which start reproducing at an early age and tend to fruit prolifically every year. In the temperate zone some late successional species, with a prolonged juvenile phase and irregular fruiting, are now spreading into semi-natural vegetation (e.g. *Quercus rubra*, *Prunus serotina* and several conifers) and this pattern may also occur in the tropics.

In term of prediction it is essential to draw list of species for which time-lags have been recorded elsewhere. Records as to the type factors, inclusive of their intensity and periodicity, that determine time-lags should be kept and compared with local conditions.

Invasive biology is so intricately linked with human history, global trade and ever decreasing transport barriers that a historical perspective is essential to understand the ecological process at hand. As pointed by Rose (1997) "nothing in biology makes sense except in the light of history" and this is especially true if one wants to understand time-lags in invasive plants.

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