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Evolution of germination strategy in the invasive species
Ulex europaeus (common gorse)

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Abstract

Aims. The study of the adaptive potential of the germination patterns of invading species enables us to identify some traits linked with their capacity to colonize new sites, and to better understand their area of distribution. The aim of the present study is to determine the germination pattern of *Ulex europaeus*, a cosmopolitan invasive species, in relation to temperature and to explore its potential evolution in a tropical invaded region since its introduction from Europe.

Methods. We studied the germination pattern of *U. europaeus* (the common gorse) to test both physical dormancy and germination capacity within the range of temperatures found in the native and invasive regions. To comprehend its germination pattern and its evolution, the rate and the speed of germination, as well as the percentage of seeds that mold during the experiment, have been compared between a native habitat, France and a habitat to which it has been introduced, the tropical island of La Reunion.

Important findings. The results show that the gorse seeds possess a very high power of germination, the ability to germinate under a wide range of temperatures and confirm the physical dormancy of the seeds (caused by seed coat impermeability). The decrease in germination from 25°C upwards, coupled with an increase in the rate of moulding help to explain its restricted distribution at altitude in tropical environments. For scarified seeds, we have not detected any difference between the two regions, neither in the percentage of germinated seeds, nor in the percentage of mould seeds. However, seeds from Réunion germinate faster at 20°C than seeds from France. For unscarified seeds ... and a greater number of seeds from Réunion are able to germinate without scarification (10-60 % for Reunion vs 0-10 % for France). These results suggest that whilst preserving the advantages of the native habitat, in Réunion gorse develops a strategy which favours the rapid occupation of new sites.

Keywords: *Ulex europaeus*, invasive species, germination, physical dormancy

INTRODUCTION

The relationship between invasiveness and species life history traits relies both on the general species characteristics and on the post-introduction evolution of the traits in introduced areas. In a meta-analysis performed on 196 non-invasive species and 125 invasive species, van Kleunen *et al.* (2010) demonstrated that the latter had generally higher values of performance-related traits, such as leaf-area allocation, shoot allocation, growth rate, size, and reproductive output.

In the introduced range, biotic and abiotic environmental conditions may be very different from those in native regions, and adaptations can occur for any favourable biological and ecological traits under the new regime of selection pressure. Phenotypic plasticity is one of the mechanisms enabling exotics to colonize large, environmentally diverse areas (Davidson *et al.* 2011; Ebeling *et al.* 2011; Griffith *et al.* 2014; Zhao *et al.* 2013), but for many species, rapid genetic evolution of traits related to growth and reproduction has been highlighted, including self-compatibility (Hao *et al.* 2010), reproductive timing (Barrett *et al.* 2008), seed production (Henery *et al.* 2010), seed mass (Buckley *et al.* 2003; Daws *et al.* 2007; Hahn *et al.* 2013), survival (Blair and Wolfe 2004), seedling emergence (Hahn *et al.* 2013), seedling height and biomass (Henery *et al.* 2010), growth rate (Blumenthal and Hufbauer 2007; Hahn *et al.* 2012; Lamarque *et al.* 2014), and biomass (Flory *et al.* 2011; Shang *et al.* 2014). In *Ulex europaeus*, previous studies have highlighted the genetic evolution of several life-history traits, especially in the early stages: i.e., seedling growth (Hornoy *et al.* 2011) and seed mass (Atlan *et al.* 2015a).

These genetic evolutions have been linked to the enemy release often observed in introduced regions (Keane and Crawley 2002) and can be explained by several hypotheses. The Evolution of Increased Competitive Ability hypothesis (EICA) states that, due to enemy release, exotic plants evolve by shifting resource allocation from defence to reproduction and/or growth (Bossdorf *et al.* 2005). The Relaxation of Genetic Correlations hypothesis (RGC) states that enemy release leads to a relaxation of the correlation selection of multi-trait defence strategies, enhancing the adaptive potential of introduced species (Hornoy *et al.* 2011).

Besides biotic factors, abiotic factors can also promote adaptations. In particular, adaptation to new local climatic conditions, temperature, rainfall and seasonality may be essential for naturalization and contribute in some cases to increased invasiveness (Barrett *et al.* 2008). Climatic adaptation often produces cline variation and several studies of invasive plants have detected latitudinal clines in life-history traits, including flowering phenology (Allan and Pannell 2009; Montague *et al.* 2008), plant size (Maron *et al.* 2004), seed production (Maron *et al.* 2004), rate or velocity of germination (Hierro *et al.* 2009; Leger *et al.* 2009), seedling growth rate (Leger *et al.* 2009) or better tolerance to local climatic conditions showing a home-site advantage (Allan and Pannell 2009).

Most of these studies have focused on reproductive output or on vegetative traits related to vigour or competitive ability, but rarely on traits related to dispersal and initial installations. In particular, less attention has been paid to seed germination patterns and evolution, although they have important demographic consequences and are directly linked to species distribution and dispersal (Hahn *et al.* 2013; Horn *et al.* 2015; Kudoh *et al.* 2007; Rejmánek 1996). Seed characteristics and germination patterns were not included in the multi-specific analyses of invasive life history traits (Godoy *et al.* 2012; van Kleunen *et al.* 2010; Leffler *et al.* 2014; Leishman *et al.* 2007; Matzek 2012), but previous studies show some trends. Invasive species tend to produce seeds that germinate faster and at a higher rate than non-invasive ones (van Kleunen and Johnson 2007; Cervera and Parra-Tabla 2009), or germinate under a wider range of environmental conditions (Cervera and Parra-Tabla, 2009;

Haukka *et al.* 2013; Pérez-Fernández *et al.* 2000) which allows them to occupy several niches rapidly. They often have heterocarpy, maximising survival in disturbed habitats (Mandák 2003), and the ability to germinate in the light, predisposing them to the colonization of disturbed and degraded areas, which is an advantage in anthropised regions (Hodgins and Rieseberg 2011; Mihulka *et al.* 2003). Their dispersion over time can be maximised by strong physical dormancy, leading to a long-lived seed bank in the soil (Mandák and Pyšek 2001; Richardson and Kluge 2008). Spatial dispersion can be increased in association with effective dispersants, which are often exotic themselves (Jordaan and Downs 2012). The evolutionary potential of germination patterns in introduced regions is also important for plant adaptation: being among the earliest life-stage transitions, it provides the context for subsequent development and predicts the environment experienced throughout the life of the plant (Donohue *et al.* 2010). Some studies have focused on the evolution of germination patterns: Erfmeier and Bruelheide (2005) for *Rhododendron ponticum*, and Blair and Wolfe (2004) for *Silene latifolia* have respectively demonstrated faster and earlier germination in the introduced region, Kudoh *et al.* (2007) showed stronger initial seed dormancy for introduced *Cardamine hirsuta* and Hierro *et al.* (2009) like Leger *et al.* (2009) demonstrated an adaptation of germination to climate conditions in the invasive range respectively for *Centaurea solstitialis* and *Bromus tectorum*. To better understand the importance of the evolution of germination patterns in invasiveness, it would be useful to study species with a wide distribution that ranges over several continents and with biological characteristics including a persistent seed bank and dormant long-lived seeds, which is the case of *Ulex europaeus* L. (Genisteeae, Fabaceae).

The perennial shrub *Ulex europaeus*, also known as common gorse, is listed by the IUCN as one of the 100 world's worst invasive species (Lowe *et al.* 2000). It is native to the European Atlantic coast (from Scotland to Portugal), under oceanic and temperate climates, and was introduced in many parts of the world especially during the 19th century, across a broad latitudinal gradient (55° S to 60 ° N) and is found in a wide range of habitats and climates (Hornoy 2012). The study of the current world distribution of gorse highlights a strong relationship between latitude and altitude in its native range and in introduced temperate zones. In its native range, it is mostly present at sea level, but under tropical climates, it is never naturalized below 1000 m, and can be found up to 3000 m in equatorial areas (Hornoy 2012). This distribution suggests that its naturalisation can occur under a wide range of climatic conditions, but is limited by warmer temperatures. Cette incapacité à s'installer dans les régions les plus chaudes pourrait s'expliquer par une difficulté à germer sous des températures élevées, car le succès de la germination dépend généralement de la température.

The objective of this study is to determine the germination pattern of gorse seeds in relation to temperature, and to explore the potential evolution of gorse in one invaded region after its introduction. We compared seeds from natural populations in Western France, a native region with a temperate climate, and from Réunion, an invaded island located in a tropical area, in order to explore the three following questions: (i) What is the germination pattern of gorse? We estimated germination rate, germination velocity and mouldy seed rate, with or without prior scarification, and under different temperatures. (ii) Is germination capacity of gorse limited by warm temperature and if so, can this limitation contribute to explain the absence of gorse at low altitude in Reunion? (iii) Did gorse germination capacity evolve between France and Reunion, and if so, do these evolutions increase gorse invasiveness?

METHODS

Study species

Ulex europaeus (Fabaceae) is a allopolyploid perennial spiny shrub that can live up to 30 years and its adult height usually varies from 1 to 4 metres (Lee *et al.* 1986). It begins to flower in its second or third year, and for several months per year (Clements *et al.* 2001). Each plant can produce ten thousand seeds per year. The seeds have an average diameter of 2 mm, and are ejected during an explosive dehiscence of pods over distance of a few metres around the maternal plant (Clements *et al.* 2001; Norambuena and Piper 2000). Gorse forms very large perennial seed banks (Hill *et al.* 2001). The majority of its seeds have a lifespan of less than 10 years under natural conditions, but in some populations, the seeds can maintain their capacity to germinate for up to 30 years (Moss 1959). The long endurance of the seeds in the soil is due to their hard and impermeable integument which induces physical dormancy (often called “hardseededness”). Under natural conditions, friction against rock and sand, soil acidity and fires contribute to the abrasion of the seed coat (Moss 1959). This allows imbibition, the first stage of germination. Seed germination takes place under suitable conditions at any time of the year, in the light or the dark (Ivens 1978).

In the native range, gorse seeds are attacked by two specific insects, *Exapion ulicis* and *Cydia succedana*. Seed predations varies and can reach over 90% in some populations (Atlan *et al.* 2010). When gorse was introduced into new areas in the 19th and 20th centuries (e.g., New Zealand, Australia, Chile, USA, Hawaii and India), very predominantly as seeds, it did not have these natural enemies. However, in most regions of the world where gorse has been declared an invasive species, seeds predators as well as others natural enemies (e.g., fungi, arachnids) have been introduced to control its spread (Hill *et al.* 2008). Réunion Island, where gorse has been introduced around 1825 (Atlan *et al.*, 2015b), is one of the few invaded regions where no biological agent has been introduced, there is no seed predators for gorse in this area to date.

Experimental material and sampling design

Two regions were selected: France, in the native European region, and Réunion, a tropical island located in the Indian Ocean (55°3E, 21°5S). Both are French (Réunion is a French overseas territory), but for simplicity, they will be referred to hereafter as "France" and "Réunion", respectively. In France, gorse is present in the western part of the country. In Réunion, gorse is now present at a range of altitudes from 1000 to 2500 m above sea level, in natural and cultivated environments. In each region, six populations were selected with a stratified sampling, which resulted in France in a selection of populations along a latitudinal gradient close to the Atlantic coast, and in Réunion along an altitudinal gradient (Table 1). In each population, seeds were collected separately from 20 individuals.

Preliminary experiments showed that the germination of the seeds is not affected by storage temperature (0 to 20°C) or by time of storage after collection (0 to 10 years): under optimal germination conditions (Atlan *et al.*, 2015a; Sixtus *et al.* 2003), seeds can attain a final germination rate of up to 90% at 30 days. In our experiments, seeds were collected during the fruiting peak between July and August 2013 in France and between July and September 2013 in Réunion. Seeds were stored in the dark, under dry conditions at 20°C, which is close to the ambient temperature and limited the risk of thermal shock during transportation. All experiments were conducted in the laboratory of the National Botanical Conservatory of Mascarin in Réunion.

Germination experiment

For each population from the two regions, batches of 100 seeds were prepared by pooling five seeds from each of the 20 individuals collected. Only complete seeds with no parasites were used. The seeds were immersed in a 50% sodium hypochlorite solution for 10 min to disinfect them, and were then rinsed under running water. A scarification treatment was performed on a subset of batches by removing a small portion of seed coat with a sterile scalpel. All seeds were then soaked in tap water for 24 h for imbibition.

The seeds were then sown in 6 cm diameter Petri dishes on VWR No. 413 filter paper, on a layer of 6 mm glass beads which covered 80% of the surface of the dishes. The constant and moderate moisture of the filter paper was enabled by the capillarity of the glass beads. The first day of germination, the number of swollen seeds (thus imbibed) was noted. The dishes were placed in a climatic enclosure in the dark at one of the following constant temperatures: 5, 10, 15, 20, 25 and 30°C for scarified seeds. The chosen temperature range for experimentation encompasses the minimum average temperature of the three coldest months in the selected regions of France (5.05 ° C) and the average maximum temperature of the three warmest months in Réunion (28.06 ° C). For unscarified seeds, the intermediate temperatures were selected: 15, 20, 25°C.

For each treatment, one batch of seeds was used, and three replicates of 30 seeds were performed per population. A seed was considered germinated when the radicle reached 2 mm. In some cases, a high number of seeds did mould, being covered by fungi belonging to *Aspergillus*, a genus commonly found in seed tegument, cotyledons and embryo. Seeds were considered as "mouldy" when they were soft and covered with fungi, and thus unable to germinate. The seeds were monitored three times a week for 45 days. At each monitoring, the germinated and mouldy seeds were counted, removed from the petri dish and destroyed (burned) to avoid seed dispersion from the laboratory.

Measurements

To study the germination capacity, the final germination rate was calculated at 45 days (Moss, 1959) and to study the sensitivity to mould, the final mould rate was also calculated at 45 days. To estimate germination velocity, two indices were selected from those developed by Ranal and Santana (2006). First, the weighted mean germination time (\bar{t}) for which the number of seeds germinated in the intervals of time established for data collection was used as the weight.

$$\bar{t} = \frac{\sum_{i=1}^k niti}{\sum_{i=1}^k ni}$$

Where ti was time from the start of the experiment to the i^{th} observation (day); ni : number of seeds germinated in the time and k last time of germination.

The second was the time required to reach 25% of germination ($Tg\ 25$). $Tg\ 25$ indicates germination velocity in the early stages while \bar{t} indicates germination velocity through the 45 days of the experiment.

Statistical analysis

Statistical analyses were performed with SAS software (SAS Institute 2005). Germination data were analysed using the GLM procedure. We used a two-level nested ANOVA in which populations were nested within regions and cross-matched with temperature. Region and temperature were considered as fixed factors and population as a

random factor. The significance of each effect was determined using type III F-statistics. Correlations were performed via a Pearson correlation coefficient (Proc CORR). Germination and mould rates were transformed using an angular function (arcsine square root) before analysis.

RESULTS

Scarified and unscarified seeds produced contrasting results and were therefore analysed separately.

Germination capacity

Scarified seeds.

After 24 hours of immersion in water, all the seeds were imbibed and swollen. Scarified seeds had the ability to germinate between 5 and 30°C, but the germination rate after 45 days depended on temperature (Table 2). Below 15°C, germination rate was close to 100%; above 15°C the germination rate declined as temperature increased, and reached 28 % at 30°C (Fig. 1). The regional effect was never significant. For the six temperatures tested, the two regions had the same germination capacity. Conversely, the population effect was highly significant, as well as the interaction between temperature and population. The variability among populations was especially significant at the three warmest temperatures.

Unscarified seeds.

After 24 hours of immersion in water only a small subset of seeds were imbibed and swollen; the germination rates obtained were much lower than for scarified seeds (Fig. 1). They still depended on temperature (Table 2), with the highest germination rates obtained at 20°C. Thus, the optimum germination temperature was different for scarified and unscarified seeds. The regional effect was significant (Table 2): the germination of populations from Réunion was significantly much higher than those from France at all temperatures (Fig. 1). The population effect was also significant on the germination rate. Another prominent trait was the high variability in the germination rate of unscarified seeds between the populations of Réunion, especially at 15°C (from 3 % for RPP to 57 % for RPE) and 20°C (from 14 % for RPP to 46 % for RCA and RMA), compared to the low variability between populations from France (see standard deviation in Fig. 1). Neither the interaction between temperature and region nor the interaction between temperature and population was significant.

Germination velocity

The time required to reach 25% of germination ($T_g 25$) could be calculated only for populations for which more than 25% of seeds had germinated after 45 days: accordingly it was calculated only for scarified seeds, and only from 5 to 25°C. The weighted mean germination time (\bar{t}) was calculated for the same sets of experiments.

For $T_g 25$ the effect of temperature was significant (Table 3): the number of days was lowest at 15°C (France 6.0 ± 1.0 d.; Réunion 6.3 ± 0.9 d.), and highest at 25°C (France 18.3 ± 1.6 d.; Réunion 13.5 ± 3.5 d). The effect of region was not significant on $T_g 25$ but interaction between temperature and region was highly significant. At the three cooler temperatures, 5, 10 and 15°C, there was no difference between France and Réunion on $T_g 25$. At the higher temperatures, 20 and 25°C, the Réunion populations reached $T_g 25$ significantly faster than the French populations (Fig. 2a and Fig. 3). Moreover, for France, $T_g 25$ was lowest and identical at 10 and 15 ° C, while for Réunion, $T_g 25$ was lowest and the

same at 10, 15 and 20°C. The effects of population and the interaction between population and temperature were both significant.

For the average germination time \bar{t} , significant effects were the same as for T_g 25: temperature, population, interaction between population and temperature and between region and temperature (Table 3). \bar{t} was lower in Réunion than in France only at 20°C.

Mould rate

Scarified seeds.

For the mould rate, the effect of temperature was significant (Table 2). Below 15°C, the mould rate was less than 10%; above this temperature, the mould rate increased as temperature increased, and reached 53±29% for France, and 44±25% for Réunion at 30°C (Fig. 4). The regional effect was not significant, but interaction between region and temperature was significant. At the coldest temperatures, populations from Réunion moulded less than populations from France, and conversely at the warmest temperatures. The effects of population and the interaction between population and temperature were significant. While all populations had equivalent mould rates below 15 ° C, the variation of mould rate between populations increased as the temperature increased above 25 ° C.

Unscarified seeds.

The mould rate of unscarified seeds was much lower than for scarified seeds. For France, it varied from 0±0% at 15°C to 3±7 % at 25°C; and for Réunion, it varied from 0.2±0.8 at 15°C to 6±8% at 25°C. The effect of the temperature was significant (Table 2): it increased when the temperature increased, although to a lesser extent than that recorded for scarified seeds (Fig. 4). Neither the region effect nor the interaction between temperature and region was significant. However, the effect of population and the interaction between population and temperature were significant. When temperature increased, the variability of the mould rate between populations increased, in both regions.

Relationship between germination and mould rate

The correlation between germination rate and mould rate was tested at 20°C, which corresponded to the temperature where both rates were high and variable. The Pearson correlation coefficient between these two rates was positive and significant (N = 12, R = + 0.74, P = 0.006), showing that the populations that had a strong ability to germinate without scarifying were also those that exhibited the most mould when they were scarified. Specifically, two population groups appeared (Fig. 5). The first group included five of the six Réunion populations, with germination rate between 38 and 45 % and a high sensitivity to mould for scarified seed. The second group included all populations from France and one Réunion population (RPP) with germination rate between 5 and 14 % and a better resistance to mould for scarified seeds.

DISCUSSION

This study demonstrated a generally high germination rate for *U. europaeus* seeds which was diminished at high temperatures. Seeds from France and Reunion had similar germination capacities but seeds from Reunion exhibited higher germination velocities at higher temperatures, and needed less scarification. This suggests that the seeds in Reunion have evolved by adapting to higher temperatures, including by modifying their germination strategy.

General germination pattern for *U. europaeus*

In all of the populations studied, more than 95% of the scarified gorse seeds were able to germinate when placed in optimal conditions, at temperatures between 5°C and 15°C. Germination rates declined below 15°C, but remained above 70% over a wide range of temperatures (5 to 25°C). A high germination rate is a characteristic feature of invasive species, enabling the swift colonisation of new environments (Baker 1974; Cervera and Parra-Tabla 2009; Flory and Clay 2009). The ability to germinate over a wide temperature range reinforces this invasive ability and permits rapid installation in differing environments (Cervera and Parra-Tabla 2009; Mihulka *et al.* 2003). Furthermore, under these optimum conditions, gorse has a particularly high germination rate, even for an invasive species, since the optimum rates described for invasive wood species show a variation of 20-30% (e.g.: *Acacia mearnsii*, Tassin 2002) up to 70-80% (e.g.: *Rhododendron ponticum*, Erfmeier and Bruelheide 2005 ; *Gleditsia triacanthos*, and *Solanum mauritianum*, Jordaan and Downs 2012). This superior capacity to germinate may be partially explained by our scarification protocol (cutting the integument with a scalpel) enabling total permeability for all the seeds. In fact, the germination rates we found are higher than those described above for gorse in experiments using other scarification methods (Gehu-Franck 1974; Sixtus *et al.* 2003). Our results show that the intrinsic germination capacity of gorse seeds is practically total, which, combined with very high seed production (Rees and Hill 2001) helps to explain its invasive capacity.

In the case of gorse, unscarified seeds do not germinate or germinate only at a relatively low level (0 to 40% depending on the temperature and the region). This strong physical dormancy complies with previous studies (Gehu-Franck 1974; Sixtus *et al.* 2003). Furthermore incubation in cold temperatures is not required for germination to begin since the seeds tested were kept at 20°C from the time they were collected. Restrictions in the distribution of gorse at the highest temperatures (Hornoy 2012) cannot be explained by a necessary breaking of dormancy by the cold in order to germinate (Baskin and Baskin 1998; Totterdell and Roberts 1979).

If both the rate and the speed of germination are taken into account, the optimal temperature range is reduced to between 10° and 15°C. At lower temperatures (5°C was the lowest temperature tested), the germination speed is reduced but the final germination rate is just as high. At higher temperatures, both the final rate of germination achieved and the speed are affected. This can partly result from the fact that, above 20°C, the rate of mouldy (and thus non-germinating) seeds strongly increased. The distribution of gorse at high altitudes, and thus its absence in lower and therefore hotter regions (Hornoy 2012), may thus be partially explained by lower germination and a greater tendency to mould at temperatures over 20°C. Nevertheless, other factors probably play a part, such as the survival of seedlings (Delereue 2013) or the need for vernalisation to trigger flowering in adults (Bonner 2008).

Comparison between France and Réunion

Seeds from the two regions under study have a similar germination capacity: germination rates of scarified seeds are identical at all the temperatures tested. On the other hand, they differ in their need for scarification, germination velocity, tendency to mould and variability between populations.

Seeds in Réunion have the capacity to germinate without scarification (10 to 60% of seeds depending on the population and the temperature) which is rarely the case in France (0 to 10% of seeds). What is more, they have a much wider range of germination temperatures reaching higher values: germination velocity after scarification is identical from 10 to 20°C, whereas for those in France it diminishes beyond 15°C. It is also at 20°C where unscarified

seeds in Réunion germinate in greater proportions. Gorse seeds in Réunion therefore germinate faster than those in France between 15 and 20°C, as a result of their reduced need for scarification and their increased speed when scarified. Studies performed on the *Rhododendron ponticum* by Erfmeier and Bruelheide (2005) gave results which are similar in part: the maximum germination rate was identical between the regions of origin and those invaded, whilst differences in germination velocity were revealed without this being linked to temperature, as had been the case in our study. A higher germination velocity reduces the period when the seed is sensitive to mould and constitutes an advantage where there is interspecific competition between seedlings (van Kleunen and Johnson 2007; Pérez-Fernández *et al.* 2000; Ross and Harper 1972). It is especially favourable in situations of colonisation (Vitalis *et al.* 2013). This may therefore have evolved in Réunion where gorse has been introduced in 1825 (Atlan *et al.*, 2015b).

Variability in germination patterns is generally the result of genetic effects in combination with maternal and environmental effects (Erfmeier and Bruelheide 2005; Rossiter 1996; Skálová *et al.* 2011). In Fabaceae in particular, the expression of genes linked with dormancy may depend on environmental conditions during the maturation of the seeds (Egley 1989; Foley 2001). The seeds for our study were collected from natural populations; the differences observed between France and Réunion may therefore be due to environmental differences between the mother plants. Nevertheless, the physical dormancy of Fabaceae seeds has a genetic basis involving a reduced number of genes (Smykal *et al.* 2014), which may enable rapid evolution. Genetic evolution of physical dormancy in accordance with local climate conditions has in fact been observed in other tropical Fabaceae (Lacerda *et al.* 2004). For gorse, faster germination in invaded areas has also been detected in seeds originating from plants cultivated in a common garden (Atlan *et al.* 2015a). This suggests that the maternal effect is not the only cause of the differences observed and that genetic effects are also involved. The greater inter-population variability in germination patterns observed in Réunion could therefore be explained by the greater climatic heterogeneity on the island compared with the Atlantic Coast of France, and could just as well result from environmental effects rather than genetic evolution.

Evolution of physical dormancy

To our knowledge, our study is the only one to have revealed a reduction in physical dormancy in an area where introduction has taken place. Nevertheless, Kudoh *et al.* (2007) have already revealed an increase in this dormancy for the annual species *Cardamine hirsuta* in the invaded areas, related to an increase of abscisic acid and leading the species to have a much wider dispersion in time and space. With gorse in Réunion, evolution towards a reduction of physical dormancy may have been facilitated by the reduced number of predators threatening the seeds. An impermeable integument helps to prevent predation by small granivorous mammals by reducing olfactory signals (Paulsen *et al.* 2013) of which very few are to be found in Réunion (there are no field mice, harvest mice or water voles, which are the main granivores in the native habitat, Quéré and Louarn 2011; UICN France *et al.* 2010). A hard integument may also restrict predation by insects, yet in Réunion there is a complete absence of the granivorous insects present in the original habitat (Hornoy *et al.* 2011). Therefore a reduction of the allocation of resources dedicated to defence (EICA hypothesis, Bossdorf *et al.* 2005) may have led to a reduction in the hardness and/or impermeability of the integument, reducing the occurrence of physical dormancy.

Absence of physical dormancy may be an advantage (Goodwin *et al.* 1999; Sakai *et al.* 2001), particularly during the course of the colonisation stage by young populations (Theoharides and Dukes 2007; Vitalis *et al.* 2013). However, physical dormancy is a

characteristic which favours endurance, dispersion and the successful establishment of invasive species in time and in space (Presotto *et al.* 2014; Smykal *et al.* 2014; Venier *et al.* 2012); furthermore, it gives protection not only against predators but also against microbial attacks (Dalling *et al.* 2011; Paulsen *et al.* 2013) and the harmful effects of winter frost (Jurado and Flores 2005). In the case of gorse, its reduction is accompanied by an increased sensitivity to mould. The balance between the advantages and disadvantages of physical dormancy therefore depends on the environmental conditions, and its variability may be interpreted as an evolutionary adaptation to climatic and biotic heterogeneity on the island (Allan and Pannell 2009; Donohue *et al.* 2010; Hahn *et al.* 2013; Hierro *et al.* 2009). Nevertheless, for a given population, the reduction of physical dormancy only affects a portion of the seeds in the population. These populations can therefore accumulate the advantages linked with strong physical dormancy (endurance, dispersion, protection against predators) and those linked with rapid germination (increased competitiveness in competitive situations), in a bet-hedging type of strategy (Olofsson *et al.* 2009; Venable 2007).

Conclusion

Germination pattern of gorse in Réunion is the result of a combination of preadaptation and postintroduction evolution, which were favourable to its invasion success. This has been also highlighted in other polyploid species as *Centaurea stoebe* (Hahn *et al.*, 2012, 2013) and *Centaurea maculosa* (Treier *et al.*, 2009). Gorse has a very high germination capacity, the ability to germinate under a wide range of temperatures, and a physical dormancy which protects the seeds and leads to wide dispersion in time. Coupled with very high annual seed production, these characteristics font partie de celles qui confèrent un fort potentiel de colonisation à l'ajonc. Nevertheless, the germination capacity of gorse is reduced at high temperatures, which may explain why its distribution is restricted to high altitudes under tropical climate. Whilst preserving the advantages of the native habitat, gorse in Réunion has developed a strategy for establishment based on faster germination at higher temperatures, and a reduction in physical dormancy on a part of the seeds, enabling maximum seizure of sites and stimulating geographic expansion (Vitalis *et al.* 2013).

The adaptive capacity of gorse in areas where it has been introduced, already revealed for other life-history traits (Atlan *et al.*, 2015a; Hornoy *et al.* 2011, 2013), is thus also present for germination. In Reunion, the new germination pattern may have been selected under the effect of selection pressures different from those in the native habitat, particularly a higher temperature and a reduced number of seed predators. The worldwide distribution of gorse includes both temperate areas where seed predators have been introduced (e.g. New-Zealand and Oregon), and tropical areas with (Hawaiï, St Helene) or without (Africa and Madagascar) introduced seed predators. It would be valuable to undertake comparative studies with these regions.

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LEGEND OF FIGURES

Fig. 1 Germination rate of *Ulex europaeus* seeds at 45 days from France and Réunion. Each point represents a population mean \pm SD (6 populations per region).

Fig. 2 Germination dynamics of *Ulex europaeus* seeds à 20°C of six populations from France, and six populations from Réunion. a: scarified seed, b: unscarified seed.

Fig. 3 Number of days required to reach 25% of germination (Tg 25) for scarified seeds of *Ulex europaeus* from France and Réunion. Each point represents a population mean \pm SD (6 populations per region).

Fig. 4 Mouldy rate of *Ulex europaeus* seeds at 45 days from France and Réunion. Each point represents a population mean \pm SD (6 populations per region).

Fig. 5 Relationship between germination rates of unscarified seeds and mouldy rates of scarified seeds of *Ulex europaeus* after 45 days at 20 ° C. Each point represents a population mean (6 populations per region).

Table 1 Main characteristics of the *Ulex europaeus* populations sampled for germination experiment.

Table 2 Results of the ANOVA testing the effects of temperature, region, and populations on germination rate, and on mould rate of *Ulex europaeus* seeds at 45 days.

Table 3 Results of the ANOVA testing the effects of temperature, region, and populations on germination velocity of scarified seeds of *Ulex europaeus*.