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Controlling gorse: Resprouting of *Ulex europaeus* after cutting in plants from native and invaded regions

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Abstract: Cutting is currently used to control invasive species. The ability of plants to produce stump sprouts, following the total or partial destruction of their aerial biomass, has strong consequences on the efficiency of this management. Here we have studied the intraspecific variability of resprouting capacities of the common gorse (*Ulex europaeus*, *ssp. europaeus*) in a common garden. We conducted a comparative study between two invaded regions (Reunion, New Zealand) and two native regions (Scotland, Brittany). Results show large intra-specific variation in the resprouting capacity of gorse, and that (1) regrowth is mainly governed by the basal architecture of individuals (2) there are differences in resprouting capacity depending on the geographic regions, but no clear trend within native and invasive areas (3) life-history traits linked with resprouting capacity also vary depending on geographic regions. These results may provide guidance for the management of gorse in invaded areas.

Keywords: Biological invasion; Resprouting; Life history traits; gorse; *Ulex europaeus*

Résumé : La lutte physique par la coupe est souvent utilisée pour contrôler les espèces envahissantes. La capacité des plantes à produire des rejets de souche, suite à la destruction totale ou partielle de leur biomasse aérienne, a de fortes conséquences sur l'efficacité de cette gestion. Nous avons étudié la variabilité intraspécifique des capacités de repousse de l'ajonc commun, (*Ulex europaeus*, *ssp. europaeus*) en jardin expérimental. Nous avons mené une étude comparative entre deux régions envahies (La Réunion, Nouvelle-Zélande) et deux régions d'origine (Ecosse, Bretagne). Les résultats montrent une grande variation intraspécifique dans la capacité de repousse de l'ajonc, et (1) que la repousse est principalement gouvernée par l'architecture basale des individus, (2) qu'il existe des différences dans la capacité de repousse selon les régions, mais pas de tendance claire entre zones natives et envahies, (3) que les traits d'histoire de vie liés à la capacité de repousse varient selon les régions. Ces résultats peuvent fournir des indications pour la gestion de l'ajonc dans les zones envahies.

Mots clés : Invasion biologique ; repousse ; traits d'histoire de vie ; ajonc ; *Ulex europaeus*.

INTRODUCTION

Biologic invasions are nowadays recognized as one of major driver of loss of biodiversity and can have consequences on economical and health fields (Riccardi et al., 2017). They also may cause many damages on natural and agronomic lands. Studies on invasive species can either focus on the invasion process or on the ways to control their expansion. Several types of control can be implemented: biological control through grazing pressure or the introduction of natural enemies, chemical control and mechanical control through fires or cutting (Rai *et al.*, 2013, Rai *et al.*, 2015). To our knowledge, very little research focuses on the effectiveness and the consequences of cutting on plant invasive species, especially on the stump sprouts, while it is a method currently used to control the expansion of plant invasive species (Rai *et al.*, 2015).

The life history traits of invasive species can evolve during the invasion process, and the differences between native and invaded regions have often been discussed (Bossdorf *et al.* 2003; Buswell *et al.*, 2011; Colautti *et al.*, 2017). Such evolutions are recorded for traits linked to reproduction (Bossdorf *et al.*, 2004), growth (Bossdorf *et al.* 2004; Buswell *et al.*, 2011) and defence against natural enemies (Felker-Quinn *et al.*, 2013). The causes of these rapid evolutions are still debated (Colautti *et al.*, 2012). However, it seems realistic to think that these changes are the result of adaptive phenomena (response to a new environment) and stochastic phenomena (genetic drift, bottlenecks). For an applied perspective, this means that the knowledge on life history traits in one regions does not help predicting the same trait in a different regions, and that management techniques must take this variability into account. Comparing the resprouting after cutting in different regions of an invasive species may provide information on the possible variations of this trait, and help the management of the species.

Here we define resprouting as the capacity of a plant to resprout after the total or partial destruction of its above-ground biomass (by cutting, grazing or fire) from dormant vegetative buds. Resprouting in plants is widely studied since it is a structural feature of ecosystems, particularly in severely disturbed environments (Bellingham *et al.*, 2000; Clarke *et al.*, 2013), meaning that it is part of the mechanisms structuring communities (Ackerly 2003). A great deal of research on resprouting compares plants that have the capacity to resprout with those that do not (Vesk *et al.*, 2012). Resprouting is therefore sometimes viewed as a bimodal trait (Pausas *et al.*, 2004; Vesk *et al.*, 2012). However, resprouting seems more like a *continuum* of strategies responding to disturbance regimes, which can differ in frequency or intensity (Bellingham *et al.*, 2000; Moreira *et al.*, 2012; Pausas *et al.*, 2014). There are trade-offs between resprouting capacity and other life history traits, such as reproduction and growth. Plants store reserves, most often in the root system, in order to be able to resprout after a severe disturbance (Wigley *et al.*, 2009). The resources allocated to these reserves are therefore no longer available to the other functions of the plant. These trade-offs have been studied extensively (Nzunda *et al.*, 2014; El-Ahmir *et al.*, 2015; Shibata *et al.*, 2016). For example, a relationships have also been shown between the capacity to resprout and investment in growth (Nzunda *et al.*, 2014) and/or reproduction (Reyes *et al.*, 2009). Sometimes, the links can be more complex. Thus, it has been demonstrated in the *Hakaea* genus (Proteaceae), a group of native Australian shrubs, that resprouting influences fecundity, which in turn affects seed size (El-Ahmir *et al.*, 2015). The relationships between resource allocation patterns, disturbance regimes and resprouting

capacity differ according to the life history trait strategies (Poorter *et al.*, 2010; Shibata *et al.*, 2016). Shade tolerance, maximum size, but also the architecture of the plant (single trunk or branched base) can influence the capacity a plant has to resprout. For example, trees and shrubs that have maintained a multi-stem architecture have more reserves in their above-ground biomass, thereby allocating less to their roots, but they are still capable of resprouting (Kubo *et al.*, 2005; Nzunda *et al.*, 2008).

Resprouting is a trait that is present in many plant families. It has often been compared between species but, to our knowledge, few studies focus on the intraspecific inter-individual variation of this functional trait (Shibata *et al.*, 2016). The common gorse (*Ulex europaeus ssp. europaeus*, Fabaceae) was considered by Reyes *et al.*, 2009 as a strong resprouter in its native range region of origin (the Northwest of the Iberian Peninsula). Common gorse has been naturally present in all Western Europe since the Neolithic (Van Zeist, 1964), and was introduced from the nineteenth century in European colonial empires throughout the world (Atlan *et al.*, 2015). It is on the “World’s Worst Invasive Alien Species” list (ISSG 2013) (ISSG-IUCN 2013) and is known to degrade habitats and cause the reduction of local biodiversity (Cordero *et al.*, 2016). Several studies have already demonstrated evolutionary changes in this species linked to its introduction into new environments. It has been shown, in experimental conditions, that seedlings from invaded regions were taller than those from native regions (Hornoy *et al.*, 2011). It has also been shown that seeds from invaded regions germinate faster than those from native regions (Udo *et al.*, 2016). Gorse also shows great inter-individual variability in most of the life history traits studied, including the flowering duration, height and plant architecture (Tarayre *et al.*, 2007; Atlan *et al.*, 2010; Hornoy *et al.*, 2012), and its genetic and reproductive systems (Hornoy *et al.*, 2013; Atlan *et al.*, 2015a).

The objective of this study is to explore geographic and intraspecific variations of resprouting after cutting in gorse, and to identify plant traits that may help predicting these variations. We have compared resprouting after cutting in an experimental garden in plants from two native regions (Brittany and Scotland) and two invaded regions (Reunion Island and New Zealand), with the objective of answering the following questions: 1) What is the capacity of gorse to survive and resprout after cutting? 2) Which life-history traits are linked with the capacity to survive and with intensity of regrowth after cutting? 3) Are the geographic differences between gorse resprouting, between regions or between native and invaded areas?

MATERIALS AND METHODS

Study species

Ulex europaeus ssp. europaeus (Fabaceae), hereafter referred to as "gorse", is a perennial spiny shrub that can live up to 20 years with an adult height that usually varies from 1 to 4 meters (Lee *et al.*, 1986). This pioneer species is an important component of heathland vegetation, and can grow on poor soil of any type, except calcareous soils (Tutin *et al.*, 1968). It is originated from Western Europe and was introduced into several parts of the world, mainly during the nineteenth century (Atlan *et al.*, 2015b). It is a cosmopolitan species with great ecological amplitude and can be found in a large ranges of latitudes - from 5° to beyond 50° north and south of the equator - and altitudes - from 0 to more than 3500m - (Hill *et al.*, 1991; Hornoy *et al.*, 2013). The flowering peak is in April, but flowering onset and flowering duration

are highly variable between individuals. Vegetative growth starts after the fruiting period and lasts approximately three months (Tarayre *et al.*, 2007; Reyes *et al.*, 2009). Multiplication by layering does not occur in this species although we observed in few occasions that a branch in contact with the soil could produce adventitious roots.

Ulex europaeus ssp. europaeus is an allopolyploid and hexaploid species with a large allelic diversity, both in its native and introduced range (Hornoy *et al.*, 2013). It exhibits great variability in life history traits, linked to growth, reproduction and defense (Tarayre *et al.*, 2007; Hornoy *et al.*, 2011; Tarayre *et al.*, 2007). Plastic responses to environmental variations have significant effect on the pod and flower productions, which reduces flower and pod sets (Delerue *et al.*, 2013; Atlan *et al.*, 2015c).

The species is a pyrophile and favours the initiation and spread of fires. After fire, gorse has very good resprouting capacities and high seed germination since fire releases seed dormancy (Zabkieski *et al.*, 1978; Hely *et al.*, 1998).

Constitution and description of the common garden

The study was performed in an experimental garden on plants grown from seeds collected in two native regions: Brittany (France) and Scotland (UK), and in two invaded regions: Reunion Island (French Overseas Territory, Indian Ocean) and New Zealand (Table 1 and Appendice 1). In each region, seeds were collected in three populations on an individual basis between 1999 and 2005. The seeds were scarified and put to germinate in Petri dishes in October 2006, then transferred to two-litre pots in a green-house in November 2006. Seedlings were grown for one year in the greenhouse under horticultural lighting, at a temperature ranging from 10 to 20°C. In November 2007, ten seedlings per population were randomly chosen and randomly transplanted in a common garden, on double rows. We kept a minimum spacing of 1.20 meters between plants of the same row, and 1.60 meters between plants of different rows. A total of 120 individuals were grown, with ten individuals per population, and three populations for each of the four regions. The common garden is located on the Campus of Rennes (Brittany, France, 48°7'3.48"N; 1°38'24.73"O), an area with several gorse populations nearby. This garden is described more thoroughly in Hornoy *et al.*, 2011.

Table 1. Main characteristics of the gorse populations sampled.

| | Region | Population | Population code | Latitude | Longitude | Elevation (m) |
|----------------------|-------------|------------------|-----------------|----------|-----------|---------------|
| Native range | | | | | | |
| | Brittany | Cap de la Chèvre | BCC | 48.1°N | 04.5°W | 0 |
| | | Château de Vaux | BCV | 48.0°N | 01.6°W | 50 |
| | | Kergusul | BKE | 48.0°N | 03.2°W | 200 |
| | Scotland | Banchory | SBA | 57.1°N | 02.5°W | 100 |
| | | Crail | SCR | 56.1°N | 02.6°W | 0 |
| | | Stirling | SST | 56.0°N | 03.9°W | 300 |
| Invaded range | | | | | | |
| | Reunion | Luc Boyer | RLB | 21.1°S | 55.6°E | 1200 |
| | | Piton Maito | RMA | 21.1°S | 55.4°E | 2200 |
| | | Piton de Brèdes | RPB | 21.2°S | 55.6°E | 1500 |
| | New Zealand | Auckland | ZAU | 37.3°S | 175.1°E | 0 |
| | | Christchurch | ZCH | 43.6°S | 172.5°E | 50 |
| | | Wellington | ZWE | 41.3°S | 174.9°E | 100 |

Experimental design and measurements

In January 2015, the plants were cut to 10 cm from the ground, leaving only the base of the stumps. We chose to cut the gorse to 10 cm, to follow the protocol of a previous study where a strong correlation between basal area at 10 cm and plant biomass was demonstrated (Delerue *et al.*, 2013). We then collected three sets of measures:

Life history traits of plants from seedling

We had the opportunity to use the measures made on the plants from seedling, done for a previous study (Hornoy *et al.*, 2011). Plant height were measured at one, two and three years, and we retained plant height at one year as an estimate of seedling vigor. Among all reproductive traits measured, we retained flowering duration, pods per shoot and seed mass (measured the third year of the plants). These traits were shown to have a genetic basis (Atlan *et al.*, 2010). We did not measure architectural and reproductive traits just before cutting, because plant branches were too intertwined.

Measurements taken on stumps

Just after cutting, in January 2015, the number of stems per stump was counted, and the diameter of each stem base was measured (maximal diameter and orthogonal diameter). Basal area (BA) of gorse stumps is a good estimate of plant biomass (Delerue *et al.*, 2013). It was calculated as following:

$$BA = \pi R^2 \text{ with } R = (\text{Max diameter} + \text{Ortho diameter})/4$$

To have an estimation of gorse architecture, we calculated a Fragmentation Index (FI) as following:

$$FI = \sum \frac{\text{Stem perimeter}}{\sum \text{Stem surface}}$$

Measurements taken on resprouting plants

One year after cutting, we recorded dead and resprouting individuals. On resprouting individuals, we measured the height of the plants, their maximum diameter and the length of the three longest sprouts. In March 2016, their flowering stage was recorded using an index based on the density and ripeness of buds, flowers and fruits (Tarayre *et al.*, 2007, and Appendice 2). This index is equal to zero when there are no reproductive items, 4 when the plants are in full bloom, 8 when all flowers turn to fruits, and 12 when all fruits are ripe. Then the plants were harvested to estimate fresh and dry biomass. The aerial part of each resprouting plant was cut, weighted, and then dried at 35°C during 14 days. That treatment reduced the biomass by 60%, a percentage already obtained after 9 days of drying; no subsequent mass reduction was obtained, showing that all water was removed.

Statistical analyses

All the statistical analyses were carried out using software R. As a first step, we compared dead and resprouting individuals. A comparison of their life history traits (from seedling and from stumps) was carried out with a Principal Component Analysis (PCA).

As a second step, we focused on resprouting individuals, and tested the effect of life history traits on regrowth capacity. Since regrowth was measured by 3 non-independent traits

(dry mass, height and diameter), we combined these three measures to create a synthetic variable named "Regrowth". "Regrowth" was calculated by 1/ transforming each variable into a mean-centered non-dimensional number and 2/ summing these three mean-centered variables. Subsequently, this synthetic variable was used to perform a mixed model analysis, where the explaining factors were the life history traits measured on plants from seedling, stump characteristics, and plant origin. "Range" (native vs invaded) and "region" were taken as fixed effects; "population" was taken as a random effect. We used the nlme (Pinheiro *et al.*, 2017) and lme4 (Bates *et al.*, 2015) packages of R. The best model was chosen using the Akaike information criterion (AIC).

As a third step, we focused on variations between the regions studied: the same mixed linear model was performed separately for each region. The homoscedasticity of the variances and the normality of the residuals were verified in all the models conceived in these analyses.

Correlations between variables were carried out with the non-parametric Spearman correlation coefficient that makes it possible to correlate quantitative and qualitative variables such as flowering stage.

RESULTS

Variability of the response to cutting

One year after cutting, among the 117 individuals cut, 84% survived and produced vegetative material, while 16% died. Among the dead plants, 74% never produced shoots, and 25% produced short shoots that dried and subsequently died. Plants that were alive one year after cutting were still alive in subsequent years. Among the resprouting plants, the variability in response to cutting was very large; the range of dry aerial biomass ranged from 55g to 3500g (562 ± 61). All resprouting individuals produced reproductive items (buds, flowers or pods): most of them flowered in the first year after cutting and the others flowered in the second year. In February 2015, one year after cutting, there was a significant positive correlation between reproductive stage (estimated from the density and ripeness of buds, flower and fruits), and resprouting aerial biomass ($N=98$, $R_{\text{Spearman}}=0.5$, $P<0.01$) or height ($N=98$, $R_{\text{Spearman}}=0.7$, $P<0.01$, Figure 1). This indicates that the biggest individuals (in term of height and aerial biomass) began to flower earlier.

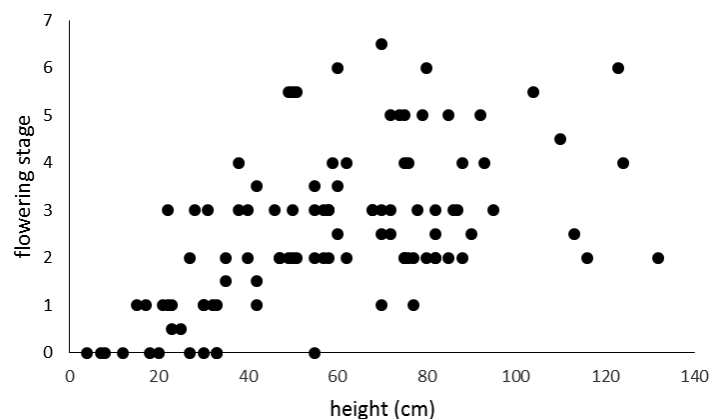


Figure 1: Relationship between flowering stage and height of resprouting individuals of *Ulex europaeus* grown in a common garden depending one year after cutting. ($N=98$, $R=0.7$, $P<0.01$.)

Resprouting capacity

To understand factors influencing gorse resprouting capacity, individuals were separated into two classes: dead and resprouting. To compare these classes a principal component analysis (PCA) was performed on variables that characterized the plants before cutting (height, reproduction) and the stumps measured just after cutting (basal area, number of stems, fragmentation).

These two classes of gorses (dead or resprouting) were differentiated according to the first and second axes of the analysis, supporting 30% and 20% of the variance, respectively. By projecting the coordinates of the individuals on axes 1 and 2, only eight individuals were on the overlap of the two ellipses representing the two classes, showing the strong discriminant power of the analysis (Figure 2, Left). For axis 3 (15% inertia) and axis 4 (10% inertia), there was overlap between classes.

The first axis is supported by high values of plant height and pod production before cutting, and weak fragmentation index of the stumps (Figure 2, Right). The second axis is supported by strong values of the number of stems and the basal area of the stumps and low values in flowering duration.

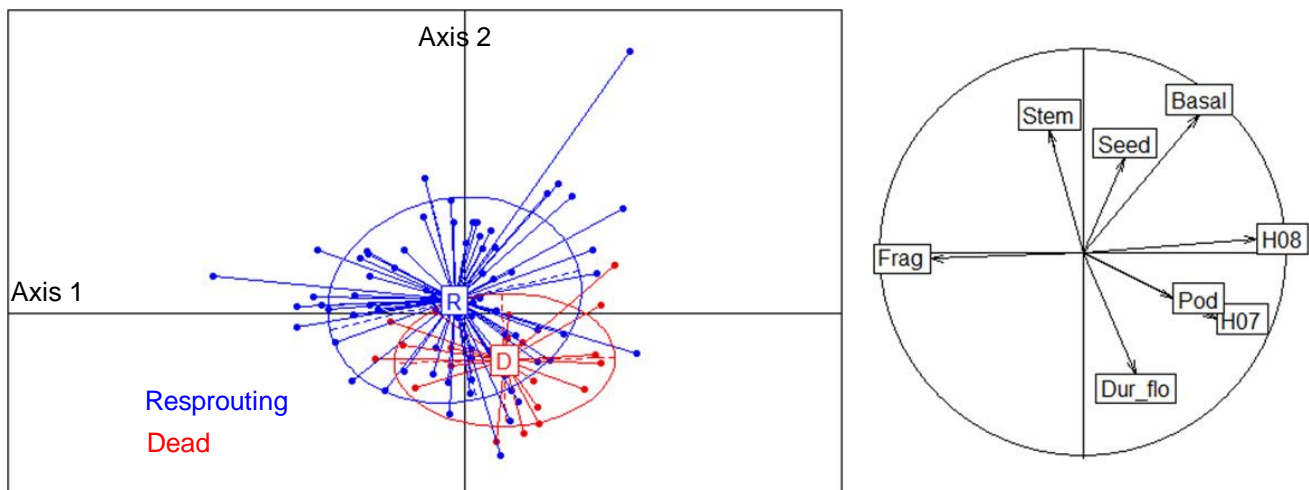


Figure 2: Results of Principal Components Analysis of individuals of *Ulex europaeus* grown in a common garden, one year after cutting.

Left: Projection of individuals on axis of PCA. Right: correlation between explanatory variables. Frag (Fragmentation Index), Stem (Number of stems), Basal (Basal area) were measured on stumps just after cutting. Pod (number of pods per shoot), seed (seed mass) Dur_flo (flowering duration), heights (H07 and H08) were measured before cutting. See text for details.

The most discriminating factor for gorse capacity to survive cutting is the number of stems per stump either counted directly or through the fragmentation Index (Figure 3). There was almost twice more stems on average for resprouting individuals than for individuals that did not survive (13. vs 7.63, T-test; N = 117, P < 0.01).

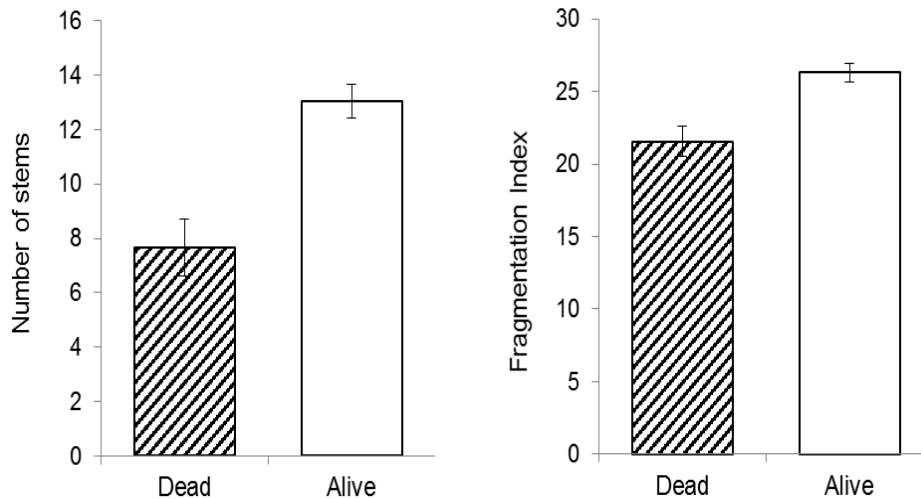


Figure 3: Comparison of number of stems and fragmentation index of dead and resprouting individuals of *Ulex europaeus* grown in a common garden (Mean \pm SE).

Traits linked with resprouting variability

In the subset of resprouting plants, the variables measured to characterize aerial parts (dry mass, height, and diameters) were strongly positively correlated (Table 2)

Table 2. Matrix of Spearman correlation coefficients between variables of resprouting. N= 97. All correlations are significant ($P < 0,001$).

| | Wet mass | Height | Diameter 1 | Diameter 2 |
|------------|----------|--------|------------|------------|
| Dry mass | 0.98 | 0.95 | 0.91 | 0.92 |
| Wet Mass | | 0.80 | 0.91 | 0.90 |
| Height | | | 0.94 | 0.91 |
| Diameter 1 | | | | 0.95 |

When all regions were pooled, regrowth of gorse depended mainly on the morphological traits of the stumps: fragmentation index (IF) and the number of stems were the only traits that had significant effect (Table 3). The effects of traits linked to vegetative growth (basal area, height) and reproduction (pod production or flowering duration) were not significant.

Effect of plant origin

The fact of plants coming from either a native or invaded range had no significant effect on regrowth, with the variability observed being mainly explained by the region of origin. The regrowth was also different between populations (nested within regions), but due to the low sample size within each population and the absence of disturbance monitoring, no attempt has been made to explain it further, and the focus has remained on the comparison between regions.

Brittany (native range) and Reunion (invaded range) had higher regrowth values than Scotland (native range) and New Zealand (invaded range), but the variation of the underlying

measurements was very high (Figure 4). The mean regrowth heights for Brittany and Reunion were similar (around 70cm), whereas for the other two other regions, it was around 50cm. Mean dry mass was the highest in Brittany (700mg), and much lower in the three other regions: 500mg for Reunion, 400mg for New Zealand and 300mg for Scotland.

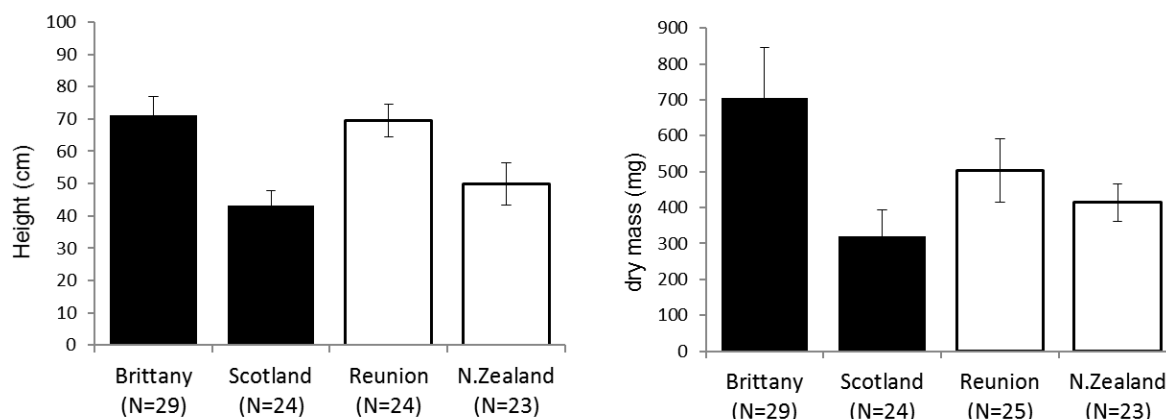


Figure 4: Height and dry mass of resprouting individuals of *Ulex europaeus* grown in a common garden depending on their region of origin, one year after cutting. Mean \pm SE.

For the four regions, the effect of seedling height had no influence on regrowth (Table 3), and the effect of the fragmentation index was highly significant: the more fragmented the stumps, the better the regrowth. For the other variables, different results were observed according to the region. In Scotland, none of the other variables had a significant effect on regrowth, in Brittany and Reunion, one other stump variable had a significant effect (number of stems for Brittany and basal area for Reunion). In New Zealand differed considerably from the three other regions: two stump variables and all reproductive variables showed significant effects: the higher the reproductive values, the lower the regrowth.

Table 3. Results of the mixed linear model on the synthetic variable of resprouting.

| | Brittany | | Scotland | | Reunion | | New | |
|----------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|
| | N=25 | | N=21 | | N=23 | | N=19 | |
| | Chi ² | P | Chi ² | P | Chi ² | P | Chi ² | P |
| Stump | | | | | | | | |
| Fragmentation Index | 10 | <0.001 | 15 | <0.001 | 9 | 0.003 | 38 | <0.001 |
| Basal area | 0.03 | 0.956 | 0.06 | 0.806 | 31 | <0.001 | 0.08 | 0.777 |
| Number of stems | 27 | <0.001 | 0.08 | 0.777 | 0.06 | 0.806 | 17 | <0.001 |
| Before cut | | | | | | | | |
| Height | 0.05 | 0.823 | 0.09 | 0.764 | 0.05 | 0.823 | 0.05 | 0.823 |
| Seed mass | 0.06 | 0.806 | 0.03 | 0.862 | 0.23 | 0.631 | 21 | <0.001 |
| Flowering duration | 0.02 | 0.887 | 7 | 0.008 | 0.08 | 0.777 | 12 | <0.001 |
| Pods per stem | 0.41 | 0.521 | 0.05 | 0.823 | 0.04 | 0.841 | 15 | <0.001 |
| R² | 0.55 | | 0.58 | | 0.55 | | 0.85 | |

DISCUSSION

The proportion of gorse individuals that survived cutting and produced stump sprouts was very high. This is consistent with previous studies reporting *Ulex europeaus ssp. europaeus* as a “strong resprouter” (Reyes *et al.*, 2009). Furthermore, the majority of plants began flowering again in the first year following cutting. The main factors linked with resprouting capacity were architectural characteristics, but other life-history traits can be involved. As with all other traits studied for this species, inter-individual variability was very strong, and significant differences were observed between regions.

A key role of plant architecture

The fragmentation index of stumps and the number of stems are the most influential factors, both on the capacity of the plants to survive cutting, and on the vigour of regrowth. The plants that did not successfully resprout were mostly those with a single trunk with large diameter. These results are consistent with other studies that showed that having several stems favours resprouting (Schafer *et al.*, 2003 and; Dacy *et al.*, 2009). The number of stems correlates positively with the photosynthetic capacity of plants, so that individuals with several stems have more resources and are able to invest more in the reserves necessary for resprouting (Cruz *et al.*, 2003; Olano *et al.*, 2006). A several-stem architecture, regarded as an adaptive response to severely disturbed environments (Paula *et al.*, 2006; Hernández *et al.*, 2011; Shibata *et al.*, 2014) could therefore be the predominant factor in the control of resprouting in gorse.

Among resprouting plants, a first hypothesis to explain variation in the vigour of regrowth could imply a trade-off between the aerial and root parts, where the largest individuals invest heavily in growth, thereby having less resources to allocate to the reserves necessary for resprouting (Bellingham *et al.*, 2000; Bond *et al.*, 2001). On the other hand, species in which individuals have optimised traits linked to photosynthesis are able to invest in vegetative growth and in underground reserves at the same time, leading to a positive relationship between growth and resprouting capacity (Paula *et al.*, 2006; Hernández *et al.*, 2011; Shibata *et al.*, 2014). In our experiment, the height at one year had no effect on the vigour of regrowth and the indirect estimate of plant biomass before cutting had an effect only in plants from Reunion, where the correlation is positive. This suggests that there is no trade-off between aerial biomass and resprouting capacity in gorse, although direct measures would have been necessary to confirm this assumption.

Link between resprouting, reproduction and competition

A link between reproductive life history traits and stump sprouts in gorse was observed in New Zealand but not in other regions. A trade-off between reproduction and resprouting has been highlighted by a large number of studies (e.g. Clarke *et al.*, 2009; Keeley *et al.*, 2012; Pausas *et al.*, 2014; El-Ahmir *et al.*, 2015; Wang *et al.*, 2014; Clarke *et al.*, 2015), but in some species, such as *Aralia elata* (Goto *et al.*, 1996) these traits were independent. Most of these studies were carried out in a natural environment, for example in dry environments in Australia (Clarke *et al.*, 2013), and Wang *et al.*, (2014) in subtropical forests in China. In contrast, our

experiment was conducted in an experimental garden where aerial competition for light was minimised with regard to the natural conditions, as was root competition for nutrients. In this context of availability of resources, the detection of links between the traits measured could be impaired.

Competition between individuals can play a role in stump resprouting capacity (Bellingam *et al.*, 2000). Following a study experiment on seed banks *in situ* conducted in Brittany, New Zealand, and Reunion (Bakker *et al.*, 2019), gorse plants were cut at 18 sites, and qualitative observations on resprouting were made two years after. In these natural sites, the mortality rate after cutting was around 80%, and appeared to be directly linked to competition for light, particularly with Poaceae. By contrast, in observations of resprouting after fire, where the burned stumps were not exposed to shade from other plants, the majority of the plants did survive and resprout. Stump resprouting capacity has been considered as an adaptation to environments that are often burned (Herrero *et al.*, 2016) and one such capacity in gorse could be interpreted as an adaptation to an environment disturbed by fire, in accordance with the pyrophilic character of the species.

Resprouting differences between regions

The resprouting capacity of plants depend on their region of origin, but there is no difference between native and invasive areas; each of these areas includes both one region with high regrowth and one with low regrowth. These results are consistent with other observations where there is no difference in regrowth after disturbance between native and non-native plants (Herrero *et al.*, 2016). However, we did find a difference in stump sprouts between regions. Due to the homogeneous conditions of the experimental garden, it is likely that these variations have a genetic basis. The strongest regrowth observed in plants from Brittany may be the result of a local adaptation, since the experiment took place in Brittany. The fact that the variables linked with regrowth differed between regions suggests that the trade-offs between life-history traits also differ between regions, as already suggested by the Release of Genetic Constraints Hypothesis (Hornoy *et al.*, 2011).

Conclusions

Gorse is recognised as a highly invasive species and has been the object of numerous control efforts, in particular by cutting. Our results provide elements to improve the efficiency of this kind of management. For example, it may be useful to cut the gorse below the height at which the stumps branch. Another important point is that stump sprouts are not affected by the same factors in different regions. The management of gorse through cutting cannot therefore be the same in all regions.

Our results show that the main factors linked with resprouting in gorse are architectural. However, they also suggest that resprouting is linked with some reproductive and vegetative life history traits. It would be very interesting to study how environmental variations could influence these components, as already shown in other species (Salk *et al.*, 2011). The capacities of stump sprouts in plants are linked to other life history strategies such as shade tolerance (Poorter *et al.*, 2010) or parasite resistance (Shibata *et al.*, 2014).

Studying the resprouting of an invasive species therefore makes it possible to provide both constructive elements with regard to their control (in this case by providing specifications on cutting height or on the differences between regions), and fundamental information on the variability of responses to disturbances in native and invaded regions.

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References

- Ackerly, D.D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164: 165-184.
- Atlan, A.; Barat, M.; Legionnet, A.; Parize, L.; Tarayre, M. 2010. Genetic variation in flowering phenology and avoidance of seed predation in native populations of *Ulex europaeus*. *Journal of Evolutionary Biology* 23: 362-371.
- Atlan, A.; Hornoy, B.; Delerue, F.; Gonzalez, M.; Pierre, J.-S.; Tarayre, M. 2015. Phenotypic plasticity in reproductive traits of the perennial shrub *Ulex europaeus* in response to shading: a multi-year monitoring of cultivated clones. *PLoS One* 10: e0137500.
- Atlan, A.; Schermann-Legionnet, A.; Udo, N.; Tarayre, M. 2015. Self-incompatibility in *Ulex europaeus*: variations in native and invaded regions. *International Journal of Plant Sciences* 176: 515-524.
- Atlan, A.; Udo, N.; Hornoy, B.; Darrot, C. 2015. evolution of the uses of gorse in native and invaded regions: what are the impacts on its dynamics and management? *Revue d'Ecologie, Terre et Vie* 70.
- Bakker, M.R.; Udo, N.; Atlan, A.; et al., Explaining the larger seed bank of an invasive shrub in non-native versus native environments by differences in seed predation and plant size. *Annals of Botany*, mcy229, <https://doi.org/10.1093/aob/mcy229>
- Bates, D.; Mächler, M.; Bolker, B.; Walker, S. 2014. Fitting linear mixed-effect models using lme4. arXiv preprint arXiv:1406.5823.
- Bellingham, P.J.; Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409-416.
- Bond, W.J.; Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in ecology & evolution* 16: 45-51.
- Bossdorf, O.; Prati, D.; Auge, H.; Schmid, B. 2004. Reduced competitive ability in an invasive plant. *Ecology Letters* 7: 346-353.
- Buswell, J.M.; Moles, A.T.; Hartley, S. 2011. Is rapid evolution common in introduced plant species? *Journal of Ecology* 99: 214-224.
- Clarke, P.J.; Knox, K.J. 2009. Trade-offs in resource allocation that favour resprouting affect the competitive ability of woody seedlings in grassy communities. *Journal of Ecology* 97: 1374-1382.
- Clarke, P.J.; Lawes, M.; Midgley, J.; Lamont, B.; Ojeda, F.; Burrows, G.; Enright, N.; Knox, K. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197: 19-35.
- Clarke, P.J.; Lawes, M.J.; Murphy, B.P.; Russell-Smith, J.; Nano, C.E.; Bradstock, R.; Enright, N.J.; Fontaine, J.B.; Gosper, C.R.; Radford, I. 2015. A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Science of the Total Environment* 534: 31-42.
- Colautti, R.I.; Barrett, S.C. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* 342: 364-366.

- Colautti, R.I.; Lau, J.A. 2015. Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Molecular Ecology* 24: 1999-2017.
- Cordero, L.R.; Torchelsen, F.; Overbeck, G.; Anand, M. 2016. Analyzing the landscape characteristics promoting the establishment and spread of gorse (*Ulex europaeus*) along roadsides. *Ecosphere* 7: e01201.
- Cruz, A.; Pérez, B.; Moreno, J.M. 2003. Plant stored reserves do not drive resprouting of the lignotuberous shrub *Erica australis*. *New Phytologist* 157: 251-261.
- Dacy, E.C.; Fulbright, T.E. 2009. Survival of sprouting shrubs following summer fire: effects of morphological and spatial characteristics. *Rangeland ecology & management* 62: 179-185.
- De Beaulieu, F.; Pouëdras, L. 2014. La mémoire des landes de Bretagne. *Skol Vreizh*.
- Delerue, F.; Gonzalez, M.; Atlan, A.; Pellerin, S.; Augusto, L. 2013. Plasticity of reproductive allocation of a woody species (*Ulex europaeus*) in response to variation in resource availability. *Annals of forest science* 70: 219-228.
- El-ahmir, S.-h.M.; Lim, S.L.; Lamont, B.B.; He, T. 2015. Seed size, fecundity and postfire regeneration strategy are interdependent in *Hakea*. *PLoS One* 10: e0129027.
- Felker-Quinn, E.; Schweitzer, J.A.; Bailey, J.K. 2013. Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). *Ecology and evolution* 3: 739-751.
- Goto, Y.; Yoshitake, T.; Okano, M.; Shimada, K. 1996. Seedling regeneration and vegetative resprouting after fires in *Pinus densiflora* forests. *Vegetatio* 122: 157-165.
- Hely C, Forgeard F. Hétérogénéité d'une lande haute à *Ulex Europaeus* L en relation avec la propagation du feu (Bretagne, France). *Canadian Journal of Botany*. 1998; 76:804-817.
- Hernández, E.; Pausas, J.; Vilagrosa, A. 2011. Leaf physiological traits in relation to resprouter ability in the Mediterranean Basin. *Plant Ecology* 212: 1959-1966.
- Herrero, M.L.; Torres, R.C.; Renison, D. 2016. Do wildfires promote woody species invasion in a fire-adapted ecosystem? Post-fire resprouting of native and non-native woody plants in central Argentina. *Environmental management* 57: 308-317.
- Hill, R.; Gourlay, A.; Martin, L. 1991. Seasonal and geographic variation in the predation of gorse seed, *Ulex europaeus* L., by the seed weevil *Apion ulicis* Forst. *New Zealand Journal of Zoology* 18: 37-43.
- Hornoy, B.; Atlan, A.; Roussel, V.; Buckley, Y.; Tarayre, M. 2013. Two colonisation stages generate two different patterns of genetic diversity within native and invasive ranges of *Ulex europaeus*. *Heredity* 111: 355.
- Hornoy, B.; Atlan, A.; Tarayre, M.; Dugravot, S.; Wink, M. 2012. Alkaloid concentration of the invasive plant species *Ulex europaeus* in relation to geographic origin and herbivory. *Naturwissenschaften* 99: 883-892.
- Hornoy, B.; Tarayre, M.; Hervé, M.; Gigord, L.; Atlan, A. 2011. Invasive plants and enemy release: evolution of trait means and trait correlations in *Ulex europaeus*. *PLoS One* 6: e26275.
- Keeley, J.E.; Bond, W.J.; Bradstock, R.A.; Pausas, J.G.; Rundel, P.W. 2011. *Fire In Mediterranean ecosystems: ecology, evolution and management*. Cambridge University Press.
- Kubo, M.; Sakio, H.; Shimano, K.; Ohno, K. 2005. Age structure and dynamics of *Cercidiphyllum japonicum* sprouts based on growth ring analysis. *Forest Ecology and Management* 213: 253-260.
- Lamont, B.B.; Wiens, D. 2003. Are seed set and speciation rates always low among species that resprout after fire, and why? *Evolutionary ecology* 17: 277-292.
- Lee, W.; Allen, R.; Johnson, P. 1986. Succession and dynamics of gorse (*Ulex europaeus* L.) communities in the Dunedin ecological district south island, New Zealand. *New Zealand journal of botany* 24: 279-292.
- Moreira, B.; Tormo, J.; Pausas, J.G. 2012. To resprout or not resprout: Factors driving intraspecific variability in resprouting. *Oikos* 121, 1213-1223.
- Nzunda, E.; Griffiths, M.; Lawes, M. 2008. Sprouting by remobilization of above-ground resources ensures persistence after disturbance of coastal dune forest trees. *Functional Ecology* 22: 577-582.

- Nzunda, E.F.; Griffiths, M.E.; Lawes, M.J. 2014. Resource allocation and storage relative to resprouting ability in wind disturbed coastal forest trees. *Evolutionary ecology* 28: 735-749.
- Olano, J.; Menges, E.; Martinez, E. 2006. Carbohydrate storage in five resprouting Florida scrub plants across a fire chronosequence. *New Phytologist* 170: 99-106.
- Paula, S.; Pausas, J. 2006. Leaf traits and resprouting ability in the Mediterranean basin. *Functional Ecology* 20: 941-947.
- Pausas, J.G.; Bradstock, R.A.; Keith, D.A.; Keeley, J.E. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85: 1085-1100.
- Pausas, J.G.; Keeley, J.E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204: 55-65.
- Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, Poorter, L.; Kitajima, K.; Mercado, P.; Chubiña, J.; Melgar, I.; Prins, H.H. 2010. Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology* 91: 2613-2627.
- Rai, P.K. 2013. *Plant invasion ecology: Impacts and Sustainable management*. Nova Science Publishers, Incorporated.
- Rai, P.K. 2015. Paradigm of plant invasion: multifaceted review on sustainable management. *Environmental monitoring and assessment* 187: 759.
- Reyes, O.; Casal, M.; Rego, F.C. 2009. Resprouting ability of six Atlantic shrub species. *Folia Geobotanica* 44: 19-29.
- Salk, C.F.; McMahon, S.M. 2011. Ecological and environmental factors constrain sprouting ability in tropical trees. *Oecologia* 166: 485-492.
- Schafer, J.L.; Just, M.G. 2014. Size dependency of post-disturbance recovery of multi-stemmed resprouting trees. *PLoS One* 9: e105600.
- Shibata, R.; Kurokawa, H.; Shibata, M.; Tanaka, H.; Iida, S.; Masaki, T.; Nakashizuka, T. 2016. Relationships between resprouting ability, species traits and resource allocation patterns in woody species in a temperate forest. *Functional Ecology* 30: 1205-1215.
- Shibata, R.; Shibata, M.; Tanaka, H.; Iida, S.; Masaki, T.; Hatta, F.; Kurokawa, H.; Nakashizuka, T. 2014. Interspecific variation in the size-dependent resprouting ability of temperate woody species and its adaptive significance. *Journal of Ecology* 102: 209-220.
- Tarayre, M.; Bowman, G.; Schermann- Legionnet, A.; Barat, M.; Atlan, A. 2007. Flowering phenology of *Ulex europaeus*: ecological consequences of variation within and among populations. *Evolutionary ecology* 21: 395-409.
- Tutin, T.G. 1968. *Flora Europaea*. Vol. 2. Rosaceae to Umbelliferae. *Flora Europaea*. Vol. 2. Rosaceae to Umbelliferae.
- Udo, N.; Tarayre, M.; Atlan, A. 2016. Evolution of germination strategy in the invasive species *Ulex europaeus*. *Journal of Plant Ecology* 10: 375-385.
- Van Zeist W (1964). A paleobotanical study of some bogs in western Brittany (Finistère), France. *Palaeohist* 10: 157-180.
- Vesk, P.A.; Westoby, M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* 92: 310-320.
- Wang, H.; Feng, H.; Zhang, Y.; Chen, H. 2014. Contrasting regeneration strategies in climax and long-lived pioneer tree species in a subtropical forest. *PLoS One* 9: e112385.
- Wigley, B.; Cramer, M.; Bond, W. 2009. Sapling survival in a frequently burnt savanna: mobilisation of carbon reserves in *Acacia karroo*. *Plant Ecology* 203: 1.
- Zabkieski JA, Gaskin S. Effect of fire on gorse seeds. *Proc.31st N. Z. Weed and Pest Control Conference*. 1978; 47-52.

Appendices

1 – The experimental Garden



2008



2009



2013



2015

2 - Flowering and fruiting stages of *Ulex europaeus*

Stage 0 : no buds

Stage 1 : buds < 2 mm long

Stage 2 : most buds 2 to 5 mm long, few buds 5 to 7 mm long

Stage 3 : most buds 5 to 7 mm long, few buds 7 to 10 mm long, few or no flowers

Stage 4 : most buds 7 to 10 mm long, several flowers

Stage 5 : full bloom: many open flowers

Stage 6 : several wilted flowers, with or without pods (small soft pods)

Stage 7 : open and wilted flowers, green hard pods, green seeds with green arils

Stage 8 : very hard pods, green seeds with yellow arils, with or without flowers

Stage 9 : green to brownish pods, yellow seeds, with or without flowers

Stage 10 : green to ripe pods, <1/3 ripe pods

Stage 11 : 1/3 to 2/3 ripe pods, few or no open pods

Stage 12 : >2/3 ripe pods, several open pods

Stage 0 : all pods open