

Assessing context-dependent survival of *Quercus glauca* seeds in a humid maritime woodland

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Abstract Whilst consumption by rodents is often invoked as a major mortality factor for large-seed species of trees, its relative importance compared with other mortality factors is poorly known. We investigated experimentally the fate of post-dispersal seeds of *Quercus glauca* under different understorey environments (areas covered by (i) a pteridophyte *Pyrrosia lingua*, (ii) a ground-vine, *Trachelospermum asiaticum* and (iii) no vegetation) from the germination stage to seedling emergence and establishment stages in humid maritime woodland. We employed a pair of caged and uncaged treatments to evaluate the impact of seed removal/predation by rodents, which allowed us to separate seed removal/predation mortality from mortality due to other factors. Effects by rodents were greater in the no-understorey habitat than in the *Pyrrosia* and *Trachelospermum* habitats at early stages of development, whilst non-rodent-associated mortality was relatively more important towards the seedling establishment stages in all habitats. In the absence of predation/removal by rodents (i.e. the caged treatment), more seedlings survived in the no-understorey habitat whilst seedlings were significantly taller in the *Pyrrosia* habitat.

In contrast, no significant difference was observed in either seed/seedling survivorship or seedling height amongst habitats where seeds/seedlings were exposed to rodent predation/removal. Overall, this study in a humid maritime woodland has revealed the temporally variable influence of mortality factors and the context-dependent survival of oak seeds/seedlings, making a contrast to observations in drier woodlands; in the no-understorey environment predation/removal effect was heavier but later survivorship was higher, whilst in vegetated environments, predation/removal was reduced but survivorship was not high.

Keywords Predation effect · Non-predation mortality · Paired experimental design · Null model · GLMM · Odds ratio

Introduction

Seed/seedling stages are ecologically critical in the life histories of many plant species (Janzen 1971; Harper 1977; Silvertown and Charlesworth 2001). In forest ecosystems, the characteristics of understorey environments are important for the fate of dispersed seeds and seedlings (Tripathi and Khan 1990; Beckage and Clark 2003). The survival of oak seeds is affected by various factors including predation (Hulme 1994, 1997; Pons and Pausas 2007; Bonal and Muñoz 2007; Muñoz and Bonal 2007; Gómez et al.

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2008), competition between plants (Wada 1993; Coll et al. 2004; Iida 2004; Itô and Hino 2007), seed size (Tripathi and Khan 1990; Osunkoya et al. 1994; Green and Juniper 2004), abiotic factors, such as light availability (Rodríguez-Calcerrada et al. 2008), humidity and soil moisture (García et al. 2002). In addition, these factors are influenced in turn by ground conditions such as litter cover (Myster and Pickett 1993; George and Bazzaz 1999a; García et al. 2002) and understorey vegetation (Rao et al. 1997; George and Bazzaz 1999a, b; Beckage and Clark 2003; Donath and Eckstein 2008). It is also known that vegetation cover at ground level functions as an ecological filter which selects post-dispersal seeds as recruits (George and Bazzaz 1999a; Caccia et al. 2006; Griffiths et al. 2007; Itô and Hino 2007; see review by Royo and Carson 2006). Apart from reducing light availability for seeds and seedlings (Wada 1993; Beckage and Clark 2003; George and Bazzaz 1999a), understorey vegetation creates refugia and feeding microhabitats for seed predators, particularly rodents (Wada 1993; Iida 2004, 2006; Itô and Hino 2007; Tsvuura et al. 2007). In general, rodents tend to forage more actively in areas where there are less risks of being attacked by vertebrate predators, which might in part be related to the height of understorey vegetation. Indeed, seed predation has been associated with relatively dense understorey vegetation, e.g. dwarf bamboos in cool temperate forests (*Sasa* spp. e.g. Wada 1993; Abe et al. 2001; Iida 2004), herbs without tree canopy (Gill and Marks 1991) and ferns in deciduous forests (George and Bazzaz 1999a).

In Mediterranean woodlands, it is known that oak seeds tend to experience elevated predation pressure from rodents in understorey habitats, but at the same time, the survival of oak seeds is enhanced by understorey vegetation that ameliorates abiotic stress, particularly in drought conditions, under the arid climate (Pérez-Ramos and Marañón 2008; Pérez-Ramos et al. 2008; Smit et al. 2008). A question arises as to whether the same situation applies to oaks in humid coastal woodlands such as those found in east Asia where drought does not normally constitutes a serious stress factor.

Whilst predation by rodents has been recognised as a major factor affecting the survival of dispersed seeds (Gill and Marks 1991; Ostfeld et al. 1997; Hulme 1997; Rousset and Lepart 2000; Iida 2006;

Gómez et al. 2008), some concerns have been raised about the evaluation of predation effects (Vander Wall et al. 2005). Although many studies attempted to identify the causes of death by examining dead and damaged seeds, the relative magnitude of predation loss (due to rodents) has rarely been assessed alongside that of non-predation mortality. Related to this, different mortality factors may operate at different times within the time scale of several weeks to months, resulting in a discordance between the optimal regeneration niche at different stages of seed/seedling development (Shupp and Fuentes 1995). Further, the true magnitude of predation mortality may be overestimated if the number of lost seeds is used simply as indicator of predation by rodents; had it not been for rodents, those (removed) seeds may have died from other mortality factors. In addition, unconsumed seeds may be hoarded or dispersed (Iida 2006; Gómez et al. 2008; Muñoz et al. 2009) and, even if partially eaten, a seed can still germinate if its embryo is intact (Steele et al. 1993; Xiao et al. 2007; Bonal et al. 2007).

The objective of this study is to evaluate the magnitude of seed predation/removal by rodents relative to that of other seed mortality factors under different understorey environments. We tested the hypothesis that the magnitude of seed/seedling losses due to predation and other factors is the same under three different types of understorey habitat. To address this issue, we conducted an experiment using a pair of caged and uncaged treatments to simultaneously assess the losses of oak seeds due to rodents and other factors from the seed germination stage through to seedling establishment in a humid temperate/subtropical maritime woodland.

Caution must be exercised when comparison is made between this and some previous studies where predation by rodents was assumed to be equated with the combined mortality (\approx number of seeds/seedlings lost from an experimental site). If no caged or predator-exclusion treatment is carried out at the same time, then it would be difficult to assess the extent of overestimation (of predation mortality). Note also that the derivation of the difference between total and non-predation mortality is facilitated by the pairing of caged and uncaged treatments placed in the same microhabitat, thereby reducing environmental noise interfering with this calculation. If caged and uncaged treatments were each randomly

placed within the study site, then the calculation would have been more troublesome, if not impossible. Thus, the experimental arrangement adopted in this study helped us detect variable patterns of predation and non-predation mortality through different stages of seed/seedling development.

Materials and methods

Study site

The study site was located on the north-western corner of the Amakusa Shimoshima Island in Kyushu, south-western Japan (32°32'N, 130°02'E). This region has been described as subtropical with summer surface water temperatures constantly reaching above 28°C (Kawai and Tokeshi 2004). The woodland occurred in a narrow sand spit, projecting into the Ariake Sea, part of the East China Sea, covering a total of 23300 m². The apical area (500 m long) of this spit, 0–3.8 m above sea level, was chosen as study site. This site was partially isolated from the basal part of the spit by a narrow (c. 10 m), barren gap where the seawater breached the land in the past and its eastern side was exposed to the effect of sea wind, whilst the western side was more protected by steep coastal hills across a small enclosed bay. Whilst the only source of freshwater into this woodland was through precipitation, humidity in the woodland was high with an annual rainfall of 1711.6 ± 140.2 mm (mean ± SE for 2005–2009). In 2008 when the main part of this study was undertaken, the rainfall between April and November was 1697 mm and the annual total 2207 mm.

Quercus glauca Thunb. is an evergreen oak species that occurs commonly in secondary forests of warm temperate East Asia including southern Japan. It was the most dominant tree species forming the canopy in the study site. We categorised three habitats based on the characteristics of understorey cover: (i) no-understorey vegetation, (ii) *Trachelospermum asiaticum* (Siebold et Zucc.) (a ground-vine species with ground-covering and climbing tendency) and (iii) *Pyrrosia lingua* (Thunb.) (a single-leaved pteridophyte species forming ground cover). The height of understorey vegetation was 10–20 cm in the *Trachelospermum* habitat and 30–40 cm in the *Pyrrosia* habitat. These vegetative covers may affect the

feeding behaviour of a major acorn consumer, a rodent *Apodemus speciosus* (Temminck), in this study site. Potential predators of *A. speciosus* were weasels, *Martes melampus melampus* (Wagner) and *Mustela itatsi* (Temminck), but their occurrences were rare or accidental. There are no other larger consumers of oak seeds, such as deer, wild boars or cattle in this maritime oak woodland (Yoko-o and Tokeshi 2011), in contrast to well-studied Mediterranean oak woodlands where mammal predators are abundant (e.g. Leiva and Fernández-Alés 2003; Gómez 2004; Pulido and Díaz 2005; Gómez and Hódar 2008; Pérez-Ramos and Marañón 2008; Pérez-Ramos et al. 2008).

Experimental design

The experiment was conducted within an area of 30 × 100 m where the three types of understorey environment (no-understorey, *Trachelospermum* and *Pyrrosia*) occurred patchily beneath a canopy (>4 m) of *Q. glauca*. Canopy openness in the study site (assessed photographically using a fish-eye lens attached to a digital camera, Yoko-o and Tokeshi 2011) was c. 10% (mean with SD, 11.3 ± 0.8% in April 2005, 9.5 ± 1.3% in June 2005). We avoided the edge areas where canopy openness was greater than that in the interior of the woodland (Yoko-o and Tokeshi 2011). Seeds for the experiment were collected in the vicinity of >20 parent trees using hanging nylon-net traps or manually from the ground in November 2007; seeds were abundant on the ground until spring 2008. Intact seeds of medium sizes (mean (±SD) fresh weight: 1.71 ± 0.35 g) were stored under outdoor conditions until use in spring 2008, and non-germinated acorns were selected by the water-floating method (e.g. Bonfil 1998; Gómez 2004; García and Houle 2005; Iida 2006) before the start of the experiment.

We employed a paired design with caged and uncaged treatments for evaluating the magnitudes of by-rodent losses of seeds/seedlings relative to that of non-rodent factors. Use of the uncaged treatment only would lead to an overestimation of the true, effective magnitude of predation, as seeds may have died, even if not consumed by rodents, for reasons other than predation by rodents. This means that the number of seeds lost from a site (or conversely, the number remaining) may not be a reliable indicator of predation mortality. On the other hand, if seeds were

handled by rodents, they are more likely to be destined to die because of either direct predation or other mortality factor(s) (e.g. mould infection, which might have caused a rodent to reject the seed). Therefore, in the present study, the number of seeds/seedlings dead or lost from the uncaged treatment was treated as total or ‘combined’ loss, and the number lost from the caged treatment as ‘non-rodent’ loss, with the difference between the former and latter being an indicator of effective loss due to rodents (see “Data analysis” section).

We set up a pair of uncaged (control) and caged treatment within a plot (50 × 50 cm) as one replication (Fig. 1) in three types of habitat. Plots under vegetation cover, i.e. in *Trachelospermum* and *Pyrrhosia* habitats, had c. 100% cover of each plant. Ten acorns, marked by marker pen, were placed on the ground surface in each treatment. A total of 13 replications were established in 13 separate plots of each habitat on 10–14 April 2008. Cages made of 5-mm stainless steel mesh were employed to exclude rodents (Fig. 1). The 4-cm height of the cage protected acorns and the basal part of a seedling shoot, but not the leaves longer than this height. This allowed insect herbivores to consume seeds/seedling. The cages did not interfere with shoot growth and leaf expansion.

Survival of seeds and seedlings was monitored daily in April and May, every two/three days in June, every week in July–November 2008, and finally in May 2010. Seed and seedling survivorship was assessed at different stages of development, i.e. germination (defined as first appearance of root through the seed coat), seedling emergence (appearance of the first leaves), and seedling establishment (shoot extending beyond the cage roof with leaves expanded). After seedling establishment, the height of each seedling was measured in July, August and October–November 2008.

Data analysis

We adopted two separate approaches to clarifying the patterns of seed mortality: (i) a null model-based analysis, and (ii) the generalised linear-mixed model. The former had an advantage of directly assessing the magnitude of difference between the paired, caged versus uncaged treatments (see Tokeshi 1999 for application of null models in general), whilst the latter allowed an integrative analysis of the effects of

three variables on overall patterns (without taking into account the paired data structure).

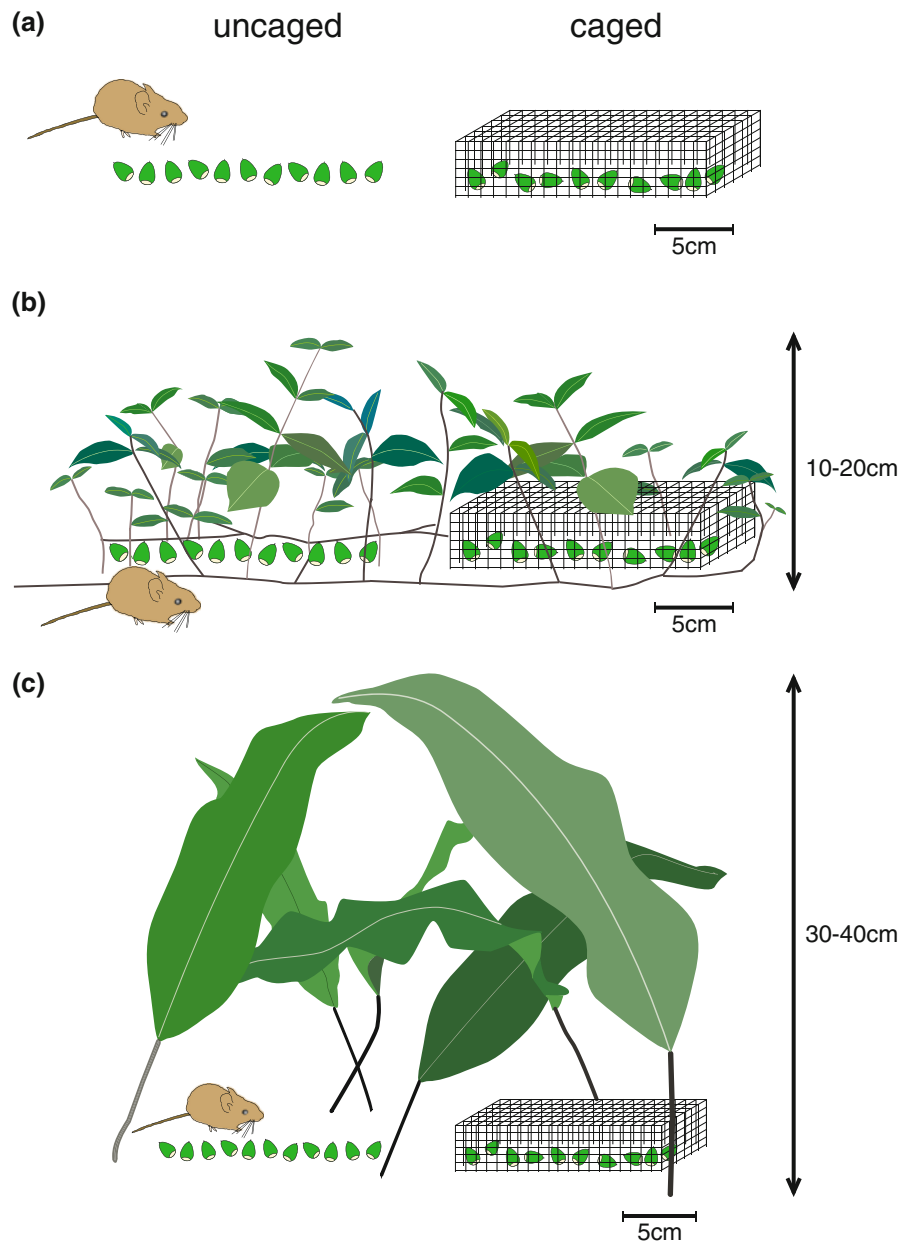
The overall effect of rodents in terms of predation/removal of seeds and seedlings (‘rodent effect’, E) was quantified using a null model-based measure that expressed the degree of departure from the situation where there was no influence of rodents on the loss of seeds/seedlings, thus

$$E = \frac{\sum (N_c - N_u)/n - M}{SD}$$

N_c and N_u are the number of seeds/seedlings remaining alive in the caged and the uncaged treatment, respectively, of a paired set, and n is the number of replicated pairs. Note that $N_c - N_u$ represents an ‘estimated maximum’ of the loss due to predation by rodents, assuming the eventual death of all seeds/seedling removed; in other words, true net mortality due to rodent predation would not exceed this value. Individual values of $N_c - N_u$ may be positive or negative, depending on the relative magnitudes of N_c and N_u and their random fluctuations. M and SD are the mean and standard deviation, respectively, of a null model (probability mass function) relating to the mean of $N_c - N_u$ in which values of N_c and N_u were generated randomly (a total of 10000 replications) in the range of $0 \leq (N_c, N_u) \leq N_{\max}$ where N_{\max} is the largest observed N_c or N_u at the start of each developmental period. As a standardised measure, E facilitates comparison across treatments and stages of development.

Generalised linear-mixed model (GLMM, see Bolker et al. 2009) was used for analysing the differences in patterns of cumulative loss of seeds/seedlings amongst habitats and between the caged and the uncaged treatments through different stages of development: (i) germination, (ii) seedling emergence, (iii) 6 months after germination, and (iv) 2 years after. We treated variation amongst 13 replications of each treatment as random effects in GLMM. Cumulative seed losses through four consecutive stages of development were modelled on the basis of binomial distributions using Gauss-Hemite quadrature (GHQ) with the logistic link, and the Akaike Information Criterion (AIC) was used for model selection (glmmML package in R, ver. 2.12.2). Variables included were three habitat types (H), caged/uncaged treatments (T), four stages of development (S) and interactions amongst these factors. For comparisons

Fig. 1 Experimental setup with three habitat types: **a** no-understorey area, **b** *Trachelospermum*, **c** *Pyrrosia*. A pair of caged and uncaged treatments, each with 10 intact seeds of *Q. glauca*, formed one replication



across habitats and treatments, odds ratios were calculated based on the derived odds of seed loss from the best-fit model; thus,

$$\frac{\pi(x)}{1 - \pi(x)} = \exp(\alpha + \beta x)$$

where $\pi(x)$ is the probability of seed loss at stage x , and the parameters α and β are treated as sums of additive components,

$$\alpha = \alpha_0 + \alpha_H + \alpha_T + \alpha_{HT}$$

$$\beta = \beta_0 + \beta_H + \beta_T + \beta_S + \beta_{HT} + \beta_{HS} + \beta_{TS} + \beta_{HTS}$$

where α_0 and β_0 are the base values and the subscripts denote variables and their interactions (note that the intercept parameter α lacks the stage component). The odds ratio (e.g. Bland and Altman 2000) was calculated for the uncaged against the caged treatment for each habitat, in order to assess the

magnitude of rodent predation. Further, the projected loss rate expressed as $\exp(\beta)$ was calculated for each fitted curve.

In addition, ANOVA with Fisher's PLSD was used for comparing seedling height between the caged and the uncaged treatments and amongst the three habitats.

Results

The rodent effect E was more pronounced in the no-understorey habitat than in *Trachelospermum* and *Pyrrosia* habitats throughout the study period, particularly at early stages of development (Fig. 2). Of the two vegetated habitats, the rodent effect was stronger in the *Trachelospermum* than in the *Pyrrosia* habitat at germination and seedling emergence stages, whilst no difference was recognisable at 6 months and 2 years after start of the experiment. Interestingly, the highest value of E for the *Pyrrosia* habitat occurred at 6 months, in contrast to the no-understorey and the *Trachelospermum* habitat.

The optimum model selected for the patterns of cumulative seed loss through the GLMM analysis (Table 1) included the three variables (habitat, treatment and stage) and two interactions (habitat \times treatment, habitat \times stage). Note that neither the treatment–stage (TS) interaction nor the habitat–treatment–stage (HTS) interaction was retained by the AIC criterion adopted in our GLMM models (which would simplify the subsequent calculation of odds ratios). Further, environmental variation amongst replications (i.e. random effect) was small

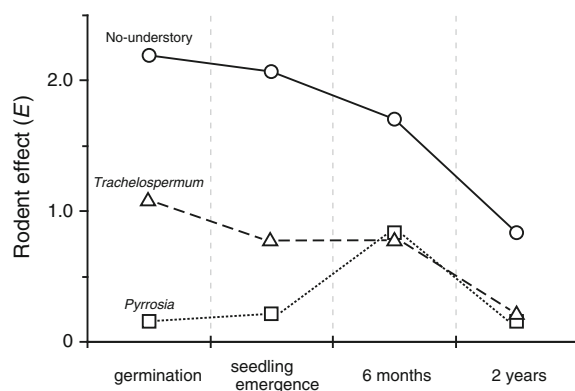


Fig. 2 Variation in rodent effect E in the three habitats: no-understorey (circular), *Trachelospermum* (triangles), and *Pyrrosia* (squares)

(mean \pm SE = 0.70 ± 0.073). The difference in cumulative seed loss between the caged and the uncaged treatments was more pronounced in the no-understorey habitat than in the *Pyrrosia* and the *Trachelospermum* habitat (Fig. 3). The odds ratio of the fitted logistic curves of the uncaged versus the caged treatment was 3.26 (95% CI: 2.15–4.97) in the no-understorey habitat, 1.97 (1.26–3.08) in the *Trachelospermum* habitat and 1.36 (0.89–2.08) in the *Pyrrosia* habitat. These values (>1.0) suggest that the magnitude of seed loss was greater in the uncaged treatment than in the caged treatment.

The projected loss rate was the same in the caged and the uncaged treatments within each habitat (i.e. no TS interaction mentioned above) but different amongst habitats. It was apparently lower in the no-understorey habitat (2.39, 95% CI: 1.98–2.88) than in the *Trachelospermum* (4.17, 3.32–5.28) and the *Pyrrosia* habitat (3.83, 3.10–4.72). These differences closely relate to comparisons of the fitted logistic curves amongst habitats for the uncaged and the caged treatments (Fig. 4), showing the advantage of the no-understorey habitat over *Trachelospermum* and *Pyrrosia* habitats towards later stages of development. Under the caged condition, this advantage was apparent as lower values of cumulative loss in the no-understorey habitat (Fig. 4a), whilst under the uncaged condition this advantage operated to nullify the initial disadvantage of heavier rodent predation.

Seedling height under the caged treatment was greater in the *Pyrrosia* habitat than in the no-understorey and the *Trachelospermum* habitat, whereas such difference was not apparent under the uncaged treatment (Fig. 5, ANOVA details in figure caption).

Discussion

It is notable that the two different methods of analysis led to broadly similar conclusions regarding the operation of rodent-associated mortality in the three habitats. The estimated maximum mortality due to rodents (the 'rodent effect') was higher in the no-understorey habitat (Fig. 2) than those in the *Trachelospermum* and *Pyrrosia* habitats. Further, the analysis of seed/seedling losses in caged and uncaged treatments clearly indicated that the influence of rodents was less pronounced under the understorey vegetation cover (*Trachelospermum* and *Pyrrosia* habitats)

Table 1 Results of model selection by AIC for a logistic regression analysis of the cumulative seed loss data using the GLMM

Model	Variables							AIC
	Habitat (<i>H</i>)	Treatment (<i>T</i>)	Stage (<i>S</i>)	<i>H</i> × <i>T</i>	<i>H</i> × <i>S</i>	<i>T</i> × <i>S</i>	<i>H</i> × <i>T</i> × <i>S</i>	
1	○	○	○	○	○	○	○	537.72
2	○	○	○	○	○	○		535.16
3	○	○	○	○		○		548.36
4	○	○	○		○	○		539.58
5	○	○	○	○	○			533.26 (selected)
6	○	○	○		○			537.85
7	○	○	○	○				546.47
8	○	○	○					552.74
9		○	○					567.54
10	○		○					582.80
11	○	○						830.59

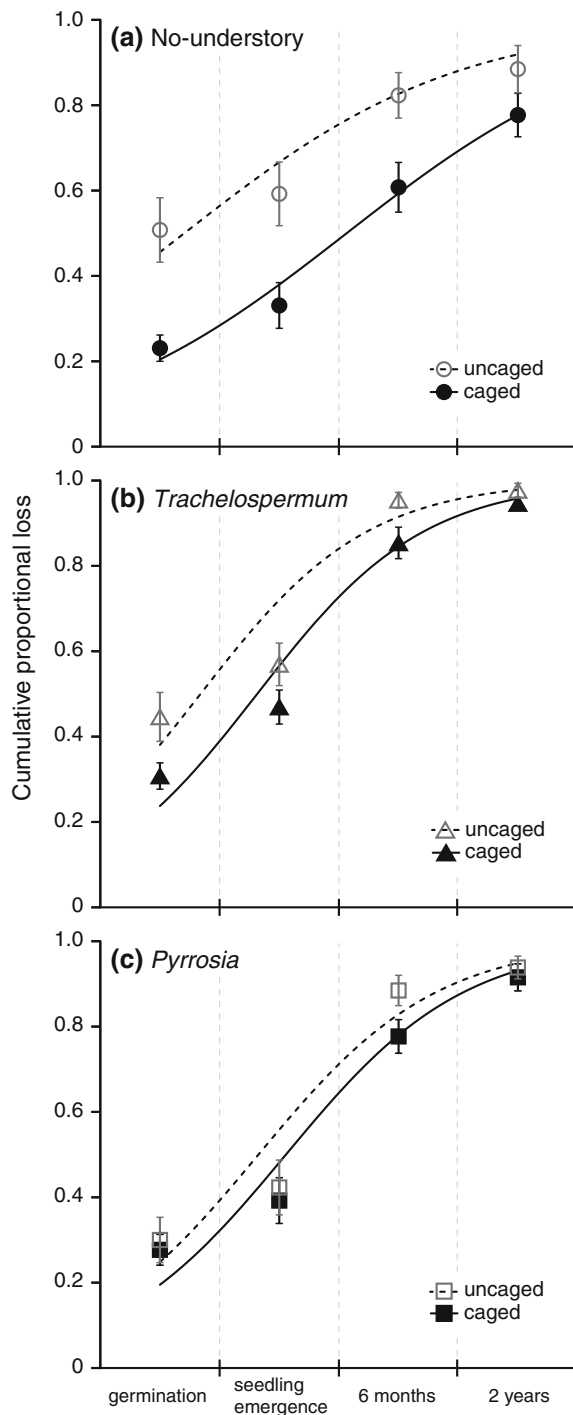
(Fig. 3). The loss due to rodents was virtually unrecognisable after 2 years of seedling growth.

These results are in contrast to previous studies on more typical inland forests where predation pressure tended to be greater in habitats with understorey vegetation than in those without (Wada 1993; Gill and Marks 1991; Manson and Stiles 1998; George and Bazzaz 1999a, b; Abe et al. 2001; Iida 2004; Tsvuura et al. 2007). In the present study, vegetation height (c. 10–20 cm in *Trachelospermum* and 30–40 cm in *Pyrrosia*) was unlikely to be an important factor given the paucity of vertebrate predators in this semi-isolated maritime woodland. Rather, the morphological characteristics of *Trachelospermum* and *Pyrrosia* may have made the habitats less favourable feeding grounds for rodents than no-understorey areas, though the exact nature of relationship between vegetation type and rodent feeding behaviour is unknown.

The results also demonstrated that different understorey environments induced apparently different responses in oak seeds and seedlings. Most notably, seedling survival was influenced by the nature of understorey habitats in the absence of predation by rodents (Fig. 4a, b), whilst such habitat effects were masked by predation in the uncaged treatment. Greater survivorship of seedlings in the no-understorey area was in concordance with a previous study (George and Bazzaz 1999b) where removal of vegetation led to better light availability and seedling survival. Variation in light availability amongst habitats must also account for differences in seedling height (Baraloto

et al. 2005). In general, lower light availability under vegetation cover encourages seedling height increase for a better acquisition of light rather than root or stem growth (Sumida et al. 1997; Baraloto et al. 2005; Rodríguez-Calcerrada et al. 2008). Thus, a greater seedling height of *Q. glauca* under *Pyrrosia* is considered as a response to reduced light under taller and denser covers, given the observed trade-off relationships between height increase and biomass/stem-diameter increase in *Q. glauca* seedlings (Sumida et al. 1997; Dickie et al. 2007). It is also notable that, in a humid environment of the studied woodland, the understorey vegetation might have aggravated the growth conditions of oak seeds through elevated humidity, thereby generating a situation opposite to what has been known in arid Mediterranean woodlands (e.g. Pulido and Díaz 2005, Gómez and Hódar 2008).

From the viewpoints of recruitment in *Q. glauca*, an intricate relation seems to exist between by-rodent mortality and non-rodent mortality associated with each habitat. In the no-understorey habitat, risks of seed predation are high but conditions for seedling growth, particularly light availability, are better (Rao et al. 1997). The opposite situation applies to habitats with understorey vegetation where less light is available due to shading (George and Bazzaz 1999a; de la Cretaz and Kelty 2002). This implies that the timing of mortality may vary in different habitats, as the initial mortality due to predation tends to be high in no-understorey habitats whereas mortality after seedling emergence may be higher in shaded understorey environments. Thus, the relative importance of



◀ **Fig. 3** Logistic regression lines fitted to cumulative losses of *Q. glauca* seeds/seedlings. *Solid lines with filled symbols*: non-rodent loss L_c (mean \pm 1SE) from caged treatments; *dashed lines with open symbols*: combined loss L_u from uncaged treatments. Parameters (α , β) of the equation, $y = \exp(\alpha + \beta x) / (1 + \exp(\alpha + \beta x))$, are **a** (−2.23, 0.87) for caged, (−1.05, 0.87) for uncaged; **b** (−2.60, 1.43) for caged, (−1.92, 1.43) for uncaged; and **c** (−2.76, 1.34) for caged, (−2.45, 1.34) for uncaged

The fact that there was an indication of increased rodent effect (E) at seedling emergence stage in the *Pyrrosia* habitats (Fig. 2) suggests that rodent predators consume the cotyledon of oak seedlings (Sato 2000; Abe et al. 2008). We also observed in the field that *A. speciosus* fed on the cotyledons of germinated seeds. Loss or damage of the cotyledon part is harmful for seedlings, leading to a lower resprouting ability (Bonfil 1998; Green and Juniper 2004, but also see Sonesson 1994; Bonal et al. 2007) and reduced tolerance of unfavourable conditions such as low light. Therefore, even if cotyledon predation by rodents may not immediately lead to the death of a seedling, its subsequent survival may be seriously compromised in understorey habitats. This might partially explain why significant differences in seedling height amongst habitats were detected in the caged treatment but not in the uncaged one, as the latter had more uniform effects of predation in all habitats.

The above considerations suggest that *Q. glauca* has broadly two possibilities for achieving its recruitment success: risking predation mortality at an early stage but growing faster in a well-lighted condition of no-understorey habitat, or reducing predation mortality but risking high seedling mortality due to shading in a vegetated understorey habitat. The advantages and disadvantages of these possibilities would change in different spatio-temporal contexts. The fact that *Q. glauca* demonstrates such context-dependent survival of young stages concurs with the observation of temporally variable allometric growth patterns (Sumida et al. 1997).

The preceding discussion points to a practical advantage of evaluating different seed loss factors simultaneously for an extended period of time, as their relative importance may shift with different spatial and temporal scales. For example, predation effects detected at an early stage of development may be completely nullified by non-predation mortality at a later stage, and vice versa. As seeds pass through

mortality due to rodent predation and that due to non-rodent factors varies spatially amongst habitats and chronologically through different stages of development.

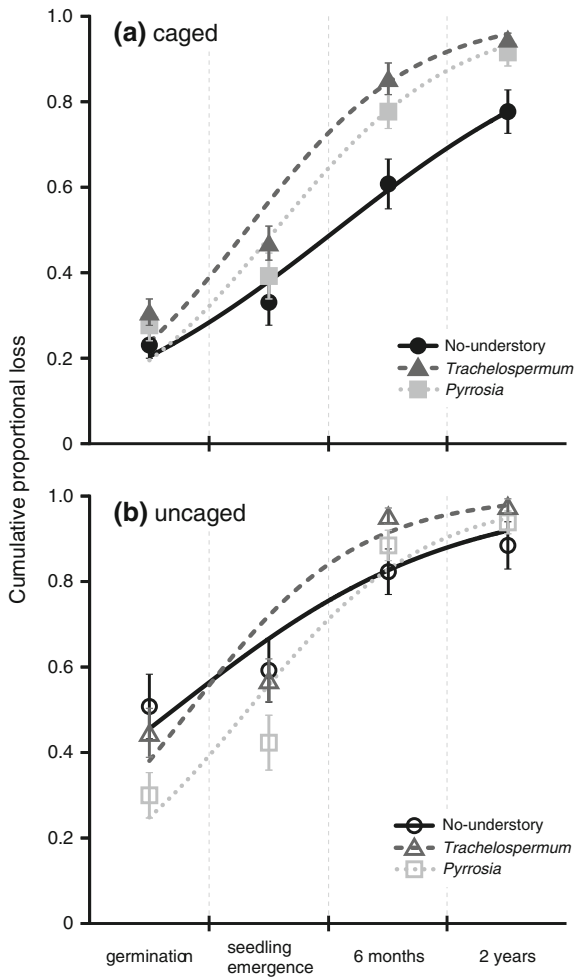


Fig. 4 Logistic regression lines fitted to cumulative losses of *Q. glauca* seeds/seedlings under **a** caged treatment (shown by filled symbols: mean \pm 1SE) and **b** uncaged treatment (shown by open symbols: mean \pm 1SE). Solid lines with circular symbols: no-understorey habitat; dashed lines with triangle symbols: *Trachelospermum* habitat; dotted lines with square symbols: *Pyrrosia* habitat. Parameters (α , β) of the equation, $y = \exp(\alpha + \beta x)/(1 + \exp(\alpha + \beta x))$, are: **a** (−2.23, 0.87) for no-understorey, (−2.60, 1.43) for *Trachelospermum*, (−2.76, 1.34) for *Pyrrosia*; **b** (−1.05, 0.87) for no-understorey, (−1.92, 1.43) for *Trachelospermum*

several critical stages in short succession, such an approach is more valuable than a single-factor, single-time analysis which may generate a misleading picture. The approach taken in the present study would contribute to a further refining of the analysis of seed/seedling mortality which is a critical aspect of plants' life history.

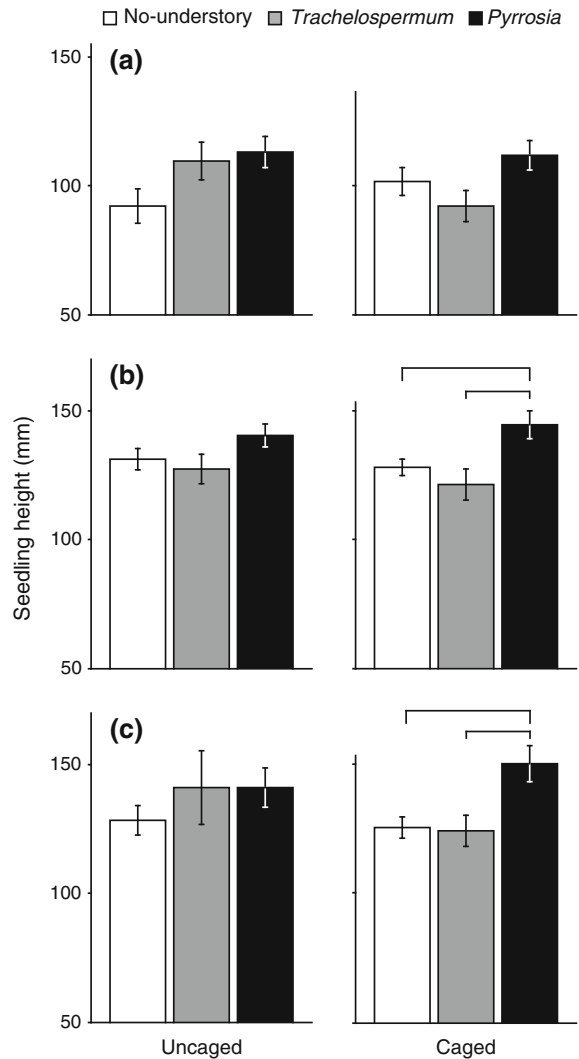


Fig. 5 Seedling height (mean \pm 1SE) in the uncaged (left) and the caged (right) treatment. **a** July, **b** August and **c** October 2008. Horizontal lines indicate treatment pairs with $P < 0.05$ (ANOVA with Fisher's PLSD, July: uncaged, $F_{2,146} = 2.805$, $P = 0.064$; caged, $F_{2,192} = 2.953$, $P = 0.055$. August: uncaged, $F_{2,87} = 1.973$, $P = 0.15$; caged, $F_{2,148} = 5.721$, $P = 0.0040$. Fisher's PLSD, $P = 0.0074$ for *Pyrrosia* versus the no-understorey, $P = 0.0022$ for *Pyrrosia* versus *Trachelospermum*, and $P = 0.33$ for *Trachelospermum* versus the no-understorey. October: uncaged, $F_{2,43} = 1.029$, $P = 0.37$; caged, $F_{2,104} = 6.333$, $P = 0.0025$; Fisher's PLSD, $P = 0.0013$ for *Pyrrosia* versus the no-understorey, $P = 0.0052$ for *Pyrrosia* versus *Trachelospermum*, $P = 0.88$ for *Trachelospermum* versus the no-understorey)

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