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Hiding from swans: optimal burial depth of sago pondweed tubers foraged by Bewick's swans

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Summary

1 We used a combination of laboratory and field experiments to test the hypothesis that the burial depth of *Potamogeton pectinatus* tubers will vary with local sediment type and swan predation pressure.

2 In the field, mortality due to predation by swans decreased linearly with burial depth (from 100% at the surface to 55% at 225 mm depth) and with sediment clay content. Average tuber size showed an eightfold increase when burial depth increased from 25 to 275 mm.

3 A laboratory experiment showed that plant emergence in spring decreased with increasing planting depth and with decreasing tuber size.

4 An optimization model combining these empirical results showed that optimal tuber survival is achieved if tuber size and burial depth increases as swan predation pressure rises. The model predicted different optimal combinations of tuber size and burial depth for sandy and clay-rich sediments.

5 A common-garden experiment showed that plants grown from large tubers produce larger tubers. Significant clonal variation in tuber size was also detected: after standardizing for tuber production, plants originating from sandy sites produced larger tubers than those originating from clay-rich sites.

6 Our results suggest the existence of spatial refuges for pondweed tubers against swan predation.

Key-words: clonal reproduction, *Cygnus columbianus bewickii*, habitat heterogeneity, *Potamogeton pectinatus*, spatial refuge

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Introduction

Following a vivid debate on whether trophic webs are primarily controlled by local resources (bottom-up forces) or by consumers (top-down forces), it is now considered likely that predator control and resource limitation may act as coregulators of population levels and community structure (Hunter & Price 1992; Power 1992; Letourneau & Dyer 1998; Pace *et al.* 1999). Ecologists are therefore now turning to an evaluation of the factors modulating their relative strengths, which depends, amongst other factors, on the efficiency with which consumers can exploit their prey. Induction of prey defences, the use of refuges by prey or patch depletion by predators will all lead to reduced edibility or availability of food, even in simple bi- and tri-trophic systems, and thus reduce top-down control (Leibold 1989; Power 1992).

The use of spatial refuges by prey reduces predator efficiency (Sih *et al.* 1985), decreasing the overall effect of predators and enhancing prey persistence (Quammen 1984; Hawkins *et al.* 1993; Stansfield *et al.* 1997). However, it usually involves a cost (e.g. due to reduced feeding rates of prey while avoiding the predator; Zaklan & Ydenberg 1997) and should therefore be an increasing function of predation risk (Sih 1982), allowing models based on postulated cost/benefit functions to predict optimal response under varying levels of resource availability and predation risk (e.g. Werner *et al.* 1983). Plants can adopt similar mechanisms to avoid being foraged by herbivores (e.g. the presence of unpalatable neighbours provides associational refuges but involves a cost in terms of increased interspecific competition, Mulder & Ruess 1998; Levine 2000).

Experimental manipulations of consumers in aquatic systems have often demonstrated cascading

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effects imposed by upper trophic levels, in which removal of predators (usually vertebrate carnivores) led to increased herbivory and decreased abundance of primary producers (Carpenter & Kitchell 1993; Brett & Goldman 1997; Agrawal 1998; Pace *et al.* 1999). Freshwater herbivore populations have rarely been manipulated (Sih *et al.* 1985), and studies on submerged vascular plants have usually been restricted to the effects of arthropod herbivores (Sih *et al.* 1985; Lodge *et al.* 1997). Fish and waterfowl grazing on pondweeds show that two-level cascading effects follow lake recovery from eutrophication (resulting in near elimination of the submerged vegetation, e.g. van van Donk 1997; Lauridsen *et al.* 1993; Søndergaard *et al.* 1996, 1997). The gregarious habits of waterfowl during migration increase foraging pressure on overwintering organs relative to summer grazing on plant leaves and shoots (Lodge *et al.* 1997; Mitchell & Perrow 1997; Idestam-Almquist 1998), compounded by the lack of potential physiological benefits, such as the release from apical dominance and removal of senescent parts of grazed plants, which do not apply when propagules are predated.

We investigated the effect of predation by Bewick's swans (*Cygnus columbianus bewickii* Yarrell, the European subspecies of tundra swan) on underground, asexual propagules (tubers) in a *Potamogeton pectinatus* L (sago pondweed) population. We predicted that the vertical distribution of these tubers might depend on both local sediment type and swan predation pressure, with burial in deep sediment layers allowing them to escape predation ('avoidance by escape', in the terminology of Saltz & Ward 2000).

We used a cost-benefit analysis (see also Ward & Saltz 1994) that is comparable with the use of optimality theory in predicting both behavioural strategies for predator avoidance (Sih 1982; Werner *et al.* 1983) and resource allocation to plant defences against herbivory (Maschinski & Whitham 1989; Ågren & Schemske 1993; Mutikainen & Walls 1995; van Dam *et al.* 1996). Tubers in deeper sediment layers are more likely to escape swan predation but their spring survival (emergence of tuber sprouts out of the sediment) will be reduced. Larger tubers are more likely to survive, but fewer can be produced per plant. The relationship between spring survival and depth varies with sediment type and the optimum depth-size combination will therefore vary between sediments, even if predation pressures remain constant.

Our model also assumes that plants developing from larger/deeper tubers will produce larger/deeper tubers at the end of the growth season. Tuber size and burial depth were strongly correlated in the field and therefore we focused on size. This could be due to either or both of non-genetical 'maternal' (environmentally induced carry-over) or genetically based (heritable clonal variation) effects. In the presence of sufficient genetic variation, selective survival of those genets whose tubers appear at optimal burial depths could result in local adaptation. It is important to note that individual plants show considerable variation in tuber size (i.e. a single plant may produce tubers of many different sizes during each growth season; Santamaría, unpublished data).

1. We carried out a field experiment to test whether tuber survival to predation by swans does increase with burial depth (hypothesis A).

2. We used a laboratory experiment to test whether spring survival increases with decreasing burial depth and with increased tuber size (hypothesis B).

3. We built a cost-benefit model to calculate optimum combinations of burial depth and tuber size and tested whether these varied with swan predation pressure and sediment type (hypothesis C).

4. We conducted a common-garden experiment to test whether plants grown from large tubers produce larger tubers (hypothesis D).

Study system

Bewick's swans migrate annually between breeding grounds in the Petchora Delta (North Russia) and overwintering sites in the Netherlands and United Kingdom (UK) (Beekman *et al.* 1996; Rees *et al.* 1997), feeding extensively *en route* on aquatic vegetation, particularly the starch-rich, underground tubers of *P. pectinatus*. They can closely track spatial variation in the availability of tubers (Beekman *et al.* 1991) and upon arrival in the Netherlands forage on *P. pectinatus* before turning to other available food sources (Beekman *et al.* 1991). The short period of use and the widespread availability of alternatives (waste agricultural crops, sedges and grasses) probably minimizes coupling between swan population dynamics and the availability of sago pondweed.

Lakes exploited by Bewick's swans are therefore likely to have scant but uniform standing crops of *P. pectinatus* (see Power 1984, 1992; Ward & Saltz 1994; Saltz & Ward 2000 for comparable situations in a freshwater and a terrestrial system). Indeed, Beekman *et al.* (1991) and van Eerden *et al.* (1997) reported increased exploitation of tuber-rich relative to tuber-poor patches until a homogeneous threshold of 2–9 g dry weight m^{-2} was reached. However, swans foraged on clay-rich soils only after depletion of tuber stocks in sandy areas (Beekman *et al.* 1991). Lower giving-up densities were also found in sandy compared with loamy lakes (van Eerden *et al.* 1997) and preferential foraging resulted in within-lake differences in giving-up densities, with sandy areas being relatively over-exploited (Nolet *et al.* 2001).

P. pectinatus is a pseudo-annual (i.e. an annual species that reproduces asexually) in which development of secondary tubers takes place at the end of the growth season and is followed by the death of the rest of the plant (including the primary tuber). Since recruitment is determined by the survival of secondary tubers (van Wijk 1988; 1989), this is a good correlate of fitness.

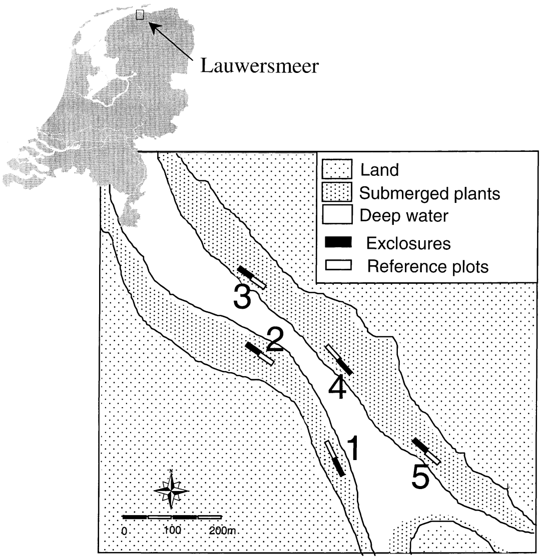

Fig. 1 Experimental design of the field experiment in the Babbelaar (Lake Lauwersmeer, the Netherlands).

Materials and methods

FIELD EXPERIMENT

We analysed the relationship between tuber mortality (due to predation by Bewick's swan or during overwintering) and burial depth of tubers, tuber size and the size × depth interaction in the Babbelaar, a Southern branch of Lake Lauwersmeer (the Netherlands). Since its creation in 1969, the lake has gradually changed from brackish to freshwater and extensive shallow areas (750 ha are less than 70 cm deep; Beekman *et al.* 1991) are dominated by *P. pectinatus*, accompanied in the Babbelaar by *Potamogeton trichoides* Cham. & Schlecht., *Zannichellia palustris* L. and *Zannichellia pedunculata* Reichenb.

A preliminary screening of swan foraging pressure and sediment characteristics (Nolet *et al.* 2001) enabled selection of five sites within the Babbelaar, *c.* 200 m apart and encompassing the observed range of both factors. At each site a 15 × 2 m exclosure and a 15 × 2 m reference plot were used to discriminate between mortality due to overwintering from the effects of swan predation (Fig. 1). The submerged exclosures consisted of a 10-cm high pvc-tubing frame covered with plastic-coated wire mesh and laid on the sediment, and were kept in place from October 1996 to April 1997. The tuber bank was sampled in early autumn (2–3 October 1996, prior to swan foraging) and in early spring (1–3 April 1997, following swan foraging and winter mortality but prior to tuber sprouting). On each date, three randomly selected, replicate points were sampled within each plot, by collecting and subsequently pooling 12 sediment cores per point (7 cm Ø, 300 mm length). The cores were divided into 50-mm sections, the number of tubers in each section was counted and the dry-weight (24 h at 70 °C) of each individual tuber was measured. Only viable, secondary tubers were included, based on visual inspection of the sprout (old, primary tubers accidentally detached from the rhizome show a broken tip) and the colour and general consistency of the tuber (which becomes brownish and soft when pathogen-infected or dead). Preliminary sampling (September 1995) had indicated that tuber presence was negligible below 300 mm.

Three additional replicate cores were taken at each site in early spring for the determination of sediment particle size (granulometry) and stored at 4 °C overnight before freeze-drying the following day. Granulometric frequencies were then determined on a Particle Sizer 3600.

Statistical analysis

Statistical analysis was performed using Statistica 5.1. for Windows (StatSoft 1995). It consisted of ANOVAS and multiple regressions, following $\log_{10}$ or arcsine (square root) transformation if the variables were not homoscedastic or the residuals did not follow a normal distribution. Differences in sediment granulometry among sites were analysed by one-way ANOVAS, followed by multiple comparisons (after adjusting the significance levels using the Dunn-Šidák method, a Bonferroni technique; Sokal & Rohlf 1995 pp. 239–240).

The effect of mortality due to overwintering and swan-predation was analysed by three-way ANOVAS ('split plot in space and time'; Steel & Torrie 1981 pp. 390–393), with site as a random factor (blocks) and treatment (exclosures vs. reference plots), and burial depth (both nested within site) and time (autumn versus spring, nested within treatment) as fixed factors.

To reduce the occurrence of missing values for tuber size (caused by few tubers surviving to spring), we pooled the three replicate samples within each site × time × treatment × depth combination. The two remaining missing values were estimated using a multiple covariance method (Steel & Torrie 1981 p. 428) and the degrees of freedom were corrected accordingly.

To estimate tuber survival following winter mortality ('winter survival') we calculated the ratio between average tuber densities (number m^{-2}) in spring and autumn, for each excluded plot and at each burial depth. Total survival (i.e. following predation and overwintering) was calculated in the same way using data from the reference plots. We assumed that winter mortality is independent of (previous) swan predation and survival to swan predation is therefore total survival divided by winter survival.

Tuber survival was then analysed by means of stepwise multiple regression on burial depth, sediment clay content (% clay, see Table 1) and their interaction (% clay × depth). Additionally, we performed a multiple *F*-test among site-specific linear regressions relating survival to burial depth (except for winter survival, which was not significantly correlated with burial depth). We used the *F*-test described in Vermaat & Hootsmans (1994) to compare the goodness-of-fit of

Table 1 Granulometric characteristics of the sediment at the five experimental sites (Babbelaar, Lake Lauwersmeer)

Site	1	2	3	4	5
Clay (%) (< 63 µm)	35.9 ± 1.7 c	16.8 ± 1.5 b	7.8 ± 0.5 a	9.3 ± 2.5 a	9.2 ± 0.7 a
Very fine sand (%) (63–113 µm)	45.7 ± 1.2 ab	47.6 ± 0.8 b	42.3 ± 1.0 a	45.0 ± 1.4 ab	47.6 ± 0.8 b
Fine sand (%) (113–262 µm)	17.4 ± 1.4 a	35.0 ± 1.5 b	48.4 ± 1.3 c	45.3 ± 2.2 c	42.5 ± 1.2 c
Medium sand (%) (262–564 µm)	0.9 ± 0.06 b	0.6 ± 0.07 a	1.3 ± 0.06 c	0.5 ± 0.06 a	0.7 ± 0.05 ab

Different letters within rows indicate significant differences (multiple comparisons, experiment-wise error rate = 0.05, comparison-wise error rate = 0.005).

separated versus pooled regressions for a predetermined set of five comparisons (CER = 0.0102, EER = 0.05; Dunn-Šidák correction). These multiple comparisons were used to select the maximum level of pooling that did not result in a significantly worse fit.

PLANT EMERGENCE EXPERIMENT

Tubers and sediment for this laboratory experiment were collected from the Babbelaar in early spring (1–3 April 1996). Tubers were washed free of sediment and stored in plastic bags at 4 °C until planted in 250-mm deep trays on 7 May 1996. Four size classes were distinguished (< 50, 51–100, 101–200 and > 200 mg fresh-weight, which resulted in averages of 35 ± 0.7, 74 ± 1.1, 142 ± 2.5 and 301 ± 11.6 mg fresh-weight, respectively; average ± SE, n = 192, 168, 120 and 96, respectively) and individual tubers from each class were randomly assigned to one of four different planting depths (75, 125, 175 and 225 mm) combined factorially with two sediment types (sandy, from site 4, and clay-rich, from site 1; Table 1). The low frequency of larger tubers in the field meant that the planned 24 replicates per tuber size per treatment could be achieved only for the smallest size class (reduced to 21, 15 and 12, respectively, for the others). Tubers of each size class were randomly distributed between the three replicated trays used for each treatment.

The 24 trays were regularly repositioned in six 100-L aquaria kept at 20 °C and illuminated 16 h per day with a surface irradiance of 150 µmol $m^{-2} s^{-1}$, i.e. optimal conditions for germination (van Wijk 1989). After 3 weeks plant material was washed free of the sediment and the biomass of the different fractions (tubers, rhizomes + roots, and stems + leaves) was determined. We regarded tubers whose sprouts grew to the sediment surface as 'survivors'. These were generally easy to distinguish from sprouted tubers whose sprouts increased in length during the experiment but died before reaching the surface. Most of these showed signs of deterioration but we also measured their sprout length.

Statistical analysis

Percentage of sprouting and survival for each tray and size class were compared by means of repeated measures ANOVAS with tuber size within each tray as the repeated measure. Some tubers did not sprout or did not survive and missing values necessitated the use of three-way ANCOVAS (with tray as a random factor and tuber size as a continuous covariable) for analysis of the biomass yield and allocation of the surviving tubers. In all cases, variables were $\log_{10}$ or arcsine (square root) transformed if necessary.

CLONAL VARIATION IN TUBER SIZE (COMMON-GARDEN EXPERIMENT)

We investigated the relative importance of non-genetical maternal effects and clonal differentiation in regulating 'offspring' tuber size, using tubers and sediment from the spring sampling in the field experiment. We selected and weighed the largest and the smallest tuber in each of these samples (three exclosed and three control per site) and estimated dry weights (initial tuber size) from a regression obtained from the remainder. Tubers were grown in individual 5.5-L pots containing a mixture of sand and clay (3 : 1 by weight) in outdoor tanks. Plants were harvested in October to determine (above- and below-ground) biomass yield, tuber production and the weight of any newly produced tubers.

Statistical analysis

Initial tuber size, biomass yield, biomass allocation and tuber production were analysed by means of two-way ANOVAS on site and 'field treatment' (i.e. exclosures versus reference plots). To account for size-mediated maternal effects, initial tuber size was entered as a covariable. Variables were $\log_{10}$ transformed if necessary.

In addition, we performed a path analysis (Sokal & Rohlf 1995; see also Silvertown & Lovett Doust 1993; Huber *et al.* 1996) using multiple regressions to evaluate (a) the effect of initial tuber size on plant biomass and (above- to below-ground) biomass allocation, and (b) the effect of these three variables on total tuber production and its allocation into tuber size and number. All variables were log-transformed. Partial correlation coefficients were calculated for all variables and coefficients of determination (i.e. percentage of variation explained by the model) were obtained for each of the three steps. Total tuber production was the only variable significantly correlated with tuber size and number and was therefore entered as a covariable in two-way ANOVAS analysing the effect of site and 'field treatment' on the size–number trade-off.

Table 2 Results of the three-way ANOVAS ('split-plot on space and time') on tuber bank characteristics

Variable		Site	Treatment	Time	Depth	Tr × Ti	Tr × De	Ti × De	Tr × Ti × De
Tuber size (dw)*	Factor d.f., Error d.f.	4, -	1, 4	1, 8	4, 12	1, 8	4, 12	4, 28	4, 28
	F	–	3.88	28.2	25.90	0.48	2.57	3.27	1.87
	P	–	0.12	**0.00072**	**0.00001**	0.51	0.092	**0.025**	0.14
Number of tubers m^{-2}	Factor d.f., Error d.f.	4, -	1, 4	1, 8	5, 20	1, 8	5, 20	5, 40	5, 40
	F	–	7.17	121.45	25.54	48.99	0.58	1.72	0.30
	P	–	0.055	**0.000004**	**0.00001**	**0.00011**	0.71	0.15	0.91
Tuber biomass (dw m^{-2})	Factor d.f., Error d.f.	4, -	1, 4	1, 8	5, 20	1, 8	5, 20	5, 40	5, 40
	F	–	10.77	162.16	34.29	43.85	4.29	2.78	1.34
	P	–	0.030	**0.00001**	**0.00001**	**0.00017**	**0.0081**	**0.030**	0.27

All variables were log-transformed (tuber size was log-transformed before averaging as the original data were strongly skewed). Significant effects ($P < 0.05$) are printed in bold. *Burial depth category '25 cm' was removed due to missing values.

Results

FIELD EXPERIMENT

Frequencies and particle sizes in the sediment varied significantly among sites ($P < 0.001$, one-way ANOVA). Multiple comparisons discriminated site 1 (clay-rich) from sites 3, 4 and 5 (sandy) with site 2 intermediate (Table 1). The sediment from site 1 had four times more clay particles and three times less fine-sand particles than the sediment from sites 3, 4 and 5 (differences in very fine and medium sand contents were of minor importance).

Tuber size, tuber-bank density and tuber-bank biomass all varied significantly with depth (Table 2). Average tuber size showed an eightfold increase (Fig. 2a) and tuber-bank biomass showed a tenfold increase (Fig. 2c) when burial depth increased from 25 to 275 mm, whereas tuber-bank density was very low in the upper 50 mm, peaked at intermediate depth and then decreased slightly with increasing burial depth (Fig. 2b). Similar patterns had been observed in September 1995 samples (data not shown).

All three measurements also decreased significantly with time (i.e. autumn versus spring; Table 2, Fig. 2). The decrease in tuber-bank density (i.e. tuber mortality) was significantly larger in the grazed plots (significant treatment × time effect; Table 2, Fig. 2b) but tuber size showed no such interaction although there was a significant time × depth effect (Table 2, Fig. 2a). Only tuber-bank biomass was affected significantly by treatment and by all two-way interactions (Table 2), decreasing significantly more over time in the grazed plots and with deeper burial (Fig. 2c). On average, swan predation reduced the tuber-bank biomass by 48% to a final value of 2–10 g dry weight m^{-2}.

Estimates of total and predation survival, but not winter survival, increased with increasing burial depth (Fig. 3). Multiple regression analysis also indicated no significant effects of clay content, burial depth or their interaction, on winter survival (Table 3a). For total survival, however, the effect of burial depth varied with sediment type (highly significant interaction in Table 3a). Survival after swan herbivory increased with increased clay content as well as with depth, although only marginally significantly for clay content (Table 3a).

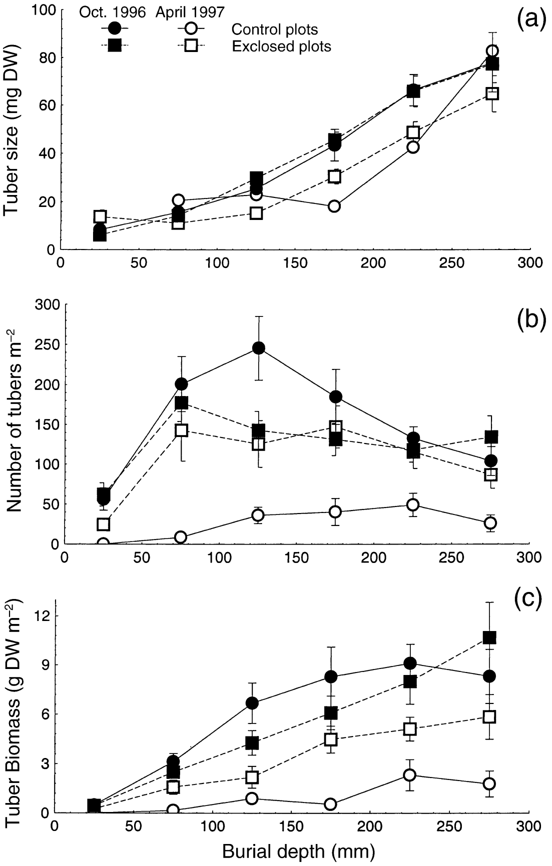

Fig. 2 Relationship between burial depth in the sediment and tuber-bank characteristics in the Babbelaar, Lauwersmeer. Bars represent standard errors ($n = 5$). DW = dry weight.

Multiple comparisons of linear regressions of survival on depth tended to discriminate sites 1 and 2 (clay-rich and intermediate) from sites 3, 4 and 5 (sandy; Table 3b). Although survival to predation increased with burial depth at sandy sites (3 to 5), it did not vary with depth at sites 1 and 2, whereas total survival showed a progressively greater increase with depth at clay-rich compared with intermediate and sandy sites. As a consequence, overall survival integrated over all burial depths increased with clay content.

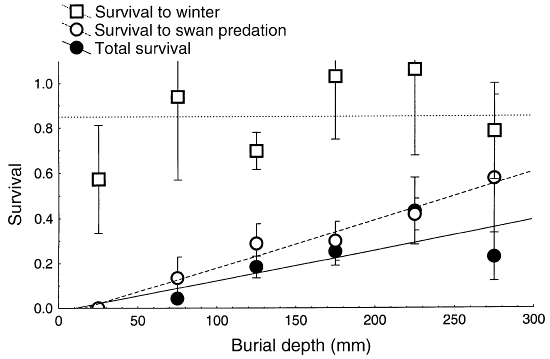

Fig. 3 Tuber survival estimated by sequential sampling inside and outside exclosures preventing predation by swans. Lines are regression fits, except for the survival to overwintering, where the average for all depths is indicated (regression was not significant, $P > 0.05$). Error bars represent standard errors ($n = 5$).

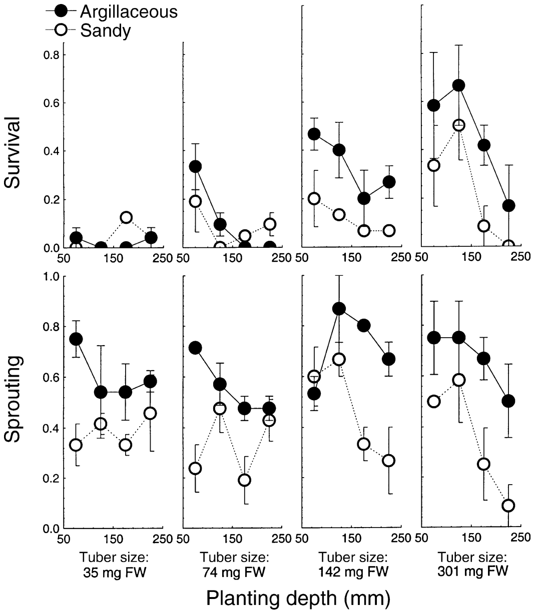

Fig. 4 The effect of experimental planting depth on the sprouting and survival of tubers of varying average fresh-weight. Bars represent standard errors ($n = 3$).

These results suggest that deep sediment layers and clay-rich areas may act as spatial refuges against extensive tuber predation by swans. Overwintering mortality, on the other hand, was fairly low (15% on average) and did not vary with burial depth.

PLANT EMERGENCE EXPERIMENT

Both tuber sprouting and survival were significantly affected by sediment type, planting depth and tuber size; survival was also significantly affected by both interactions including tuber size (Table 4). Survival and sprouting were higher in the clay-rich sediment, but only at larger sizes (Fig. 4). Survival and sprouting decreased with increasing burial depth, particularly for the large tubers (Fig. 4). Survival was higher at larger sizes (Fig. 4). Overall, survival of the smaller tubers was negligible, but for larger tubers it decreased strongly with planting depth and was 30–80% lower in the sandy sediment.

Once the plants succeeded in reaching the sediment surface, biomass yield was significantly affected by tuber size (Table 4; biomass increased with initial tuber size) and the interaction of sediment type and planting depth was marginally significant (Table 4; yield decreased with depth more strongly in clay-rich sediment). Biomass allocation into above- and below-ground parts

Table 3 (a) Stepwise multiple regression analysis of the effect of sediment composition (% clay from granulometric analysis) and burial depth (in cm) on tuber survival. (b) Multiple comparisons among site-specific linear regression fits relating survival to burial depth

(a) Dependent variable	Intercept B ± SE, p	Clay (%) B ± SE, p	Burial depth B ± SE, p	Clay × Depth B ± SE, p	Regression model F(d.f.), adj.r^2, p
Survival after winter	1.30 ± 0.39 $P = 0.002$	–0.038 ± 0.020 $P = 0.074$	–0.0025 ± 0.0023 $P = 0.27$	$(22 \pm 12)*10^{-5}$ $P = 0.075$	1.42(3.26) 0.04 $P = 0.26$
Survival after predation	–0.19 ± 0.15 $P = 0.23$	0.0122 ± 0.006 $P = 0.062$	0.0020 ± 0.0007 $\mathbf{P = 0.015}$	–	5.92(2.26) 0.26 $\mathbf{P = 0.008}$
Total survival	0.063 ± 0.051 $P = 0.22$	–	–0.0045 ± 0.0037 $P = 0.24$	$(83 \pm 17) \times 10^{-6}$ $\mathbf{P = 0.00005}$	15(2.27) 0.51 $\mathbf{P = 0.00003}$

(b) Dependent variable	Sites pooled	Survival after predation	Survival predation + winter
Summary of comparisons*:		1 2 3 4 5	1 2 3 4 5
'Best' regression model†	(1 + 2)	$S = 0.0041 \times D - 0.109$, $r^2 = 0.43$, $P = 0.28$	$S = 0.0021 \times D - 0.035$, $r^2 = 0.45$, $\mathbf{P < 0.02}$
	(3 + 4 + 5)	$S = 0.00084 \times D + 0.015$, $r^2 = 0.23$, $\mathbf{P < 0.04}$	$S = 0.00089 \times D + 0.00003$, $r^2 = 0.24$, $\mathbf{P < 0.04}$

Significant terms and regression models ($P < 0.05$) are printed in bold, marginally significant terms ($P < 0.10$) are underlined. *Summary of five comparisons (EER = 0.05, CER = 0.0102), each based on an F-test comparing the RSS of separated versus pooled regressions. †Maximal amount of separated regressions that result in a significantly lower RSS than pooled regressions.

Table 4 Effects of sediment type, planting depth and tuber size on (a) sprouting and survival (three-way ANOVA) and (b) biomass yield and allocation (three-way ANCOVA) of *P. pectinatus*. (a)

	d.f. Effect	d.f. Error	F	P-level
(a)				
Sprouted (%)				
Sediment	1	16	55.12	**0.000001**
Depth	3	16	6.16	**0.0055**
Tuber size	3	48	2.82	**0.049**
Sediment × depth	3	16	1.44	0.27
Sediment × tuber size	3	48	0.35	0.79
Depth × tuber size	9	48	1.64	0.13
Sediment × depth × tuber size	9	48	1.67	0.12
Survival (%)				
Sediment	1	16	12.24	**0.0030**
Depth	3	16	7.34	**0.0026**
Tuber size	3	48	17.40	**0.000001**
Sediment × depth	3	16	0.64	0.60
Sediment × tuber size	3	48	3.76	**0.017**
Depth × tuber size	9	48	3.03	**0.0059**
Sediment × depth × tuber size	9	48	0.34	0.96
(b)				
Vegetative biomass*†				
Sediment	1	12	1.75	0.21
Depth	2	12	0.0029	0.99
Tray (random)	12	–	–	–
Sediment × depth	2	12	3.38	0.068
Covariable: tuber size†	1	64	85.47	**0.000001**
	B ± SE = 0.82 ± 0.09, $r^2 = 0.57$			
Shoot : root ratio*†				
Sediment	1	12	1.45	0.25
Depth	2	12	0.96	0.41
Tray (random)	12	–	–	–
Sediment × depth	2	12	0.59	0.57
Co-variable: tuber size†	1	63	1.71	0.19
	B ± SE = 0.16 ± 0.09, $r^2 = 0.05$			

Significant effects ($P < 0.05$) are printed in bold, marginally significant effects ($P < 0.10$) are underlined. *Only tubers that survived and grew new plants. †Log-transformed.

was not affected by sediment type, tuber burial depth or tuber size (Table 4).

OPTIMIZATION MODEL

In order to explore which size–depth combination would maximize survival in different sediment types under the observed predation pressure, we constructed a simple model and fitted it to the empirical results described above. The model assumes that the transition from tuber production during one season to growing plants in the next season is governed by three independent events: surviving predation by swans, winter survival and successful sprouting.

Escape from predation increases linearly with depth but is independent of sediment type and tuber size (Fig. 3). However, as the probability that a tuber survives must be between 0 and 1, we modelled it by the function:

$$f(d) = \max\{0, 1 - \mathrm{a} \cdot \exp(-\beta d)\} \qquad \text{eqn 1}$$

where d represents burial depth (in mm) and β represents predation pressure. For sufficiently low values of β ($\beta < 0.005$), $f(d)$ is essentially linear in the studied depth range (0–250 mm). Higher values of β correspond to decreasing predation pressures.

Winter survival (WS) appears to be independent of tuber size, burial depth and sediment type and is therefore assumed to be constant.

The probability that a tuber of size s (in mg freshweight) buried at a depth d (in mm) sprouts successfully in spring is modelled as

$$g(d,s) = c(s) - b(s) \cdot d \qquad \text{eqn 2}$$

where

$$c(s) = \max\{0, 1 - \mathrm{c} \cdot \exp(-\gamma s)\} \qquad \text{eqn 3}$$

$$b(s) = \mathrm{b}_1 + \mathrm{b}_2 \cdot s \qquad \text{eqn 4}$$

The relationship between maximum spring survival (i.e. the probability of successfully sprouting from the sediment surface) and tuber size is determined by c and γ. Different values of b_1 and b_2 describe how the rate at which survival decreases with burial depth varies with tuber size.

Overall survival, the product of $f(d) \times WS \times g(d,s)$, showed a unimodal relationship with burial depth, with optimal survival occurring at increasing depths as tuber size increased. Assuming that the cost of building up a tuber was directly proportional to its biomass (fw), a plant producing tubers of a fixed size and burial depth would be expected to leave a number of offspring proportional to W = (tuber survival)/(tuber fw). This assumption is based on the comparable construction cost found for propagules of different submerged plant species (Spencer *et al.* 1997) and on the homogeneous chemical composition of *P. pectinatus* tubers of varying sizes (van Eerden *et al.* 1997; Santamaría, unpublished data).

Parameter values were estimated using an algorithm that minimized the residual sum of squares. Equation 1 was fitted to our field data relating survival to burial depth (Fig. 3) and equations 2, 3 and 4 were fitted to our experimental data relating spring survival to burial depth and tuber size (Fig. 4). Fits for equation 4 were subjected to the constraint that the maximum depth at which a tuber can sprout is an increasing function of tuber size (i.e. $c(s)/b(s)$ is an increasing function of s). We estimated parameters separately for the sandy and clay-rich sediments so that we could explore whether the relationship between survival, burial depth and tuber size varies with sediment type under the 'observed' predation pressure. We also simulated increasing predation pressure by decreasing the value of β while keeping all other parameters constant to test whether optimal tuber size, s^*, and optimal burial depth, d^*, for survival increase. Estimated s* and d^* for a given set of parameter values were those positive (> 0) values that maximized the fitness function W.

In a non-grazed situation, tubers placed in the uppermost sediment layers have the highest fitness (W) (Fig. 5a; the minimal value of d^* is determined by the value of β chosen to represent a no-predation situation) but optimal tuber sizes are more than twofold larger in sandy sediment (Fig. 5a). Under predation, the highest fitness (W) is found at intermediate depths (d^* = 130–150 mm) and for medium to large tuber sizes (s^* = 150 mg fw in argillaceous sediment, s^* = 240 mg fw in sandy sediment; Fig. 5a). These predictions are consistent with the shift in tuber-biomass allocation in the field (from small to larger tubers) found along the gradient of increasing predation pressures and decreasing clay content (predation pressure was lowest at site 1, intermediate at 2, 3 and 5, highest at 4; data not shown), although W peaked at smaller burial depths than did biomass. Size-selective mortality, which could have accounted for this discrepancy, was not included in the model as it did not result in significant changes in tuber size (no significant 'treatment × size × depth' interaction in the three-way ANOVA, possibly due to its lower discriminatory power caused by the presence of missing values; Table 2). However, in swan-predated plots, surviving tubers are smaller at 175 and 225 mm (Fig. 2a), probably due to selective predation on large tubers when the latter are present (as confirmed by experiments with captive swans; Nolet, unpublished data).

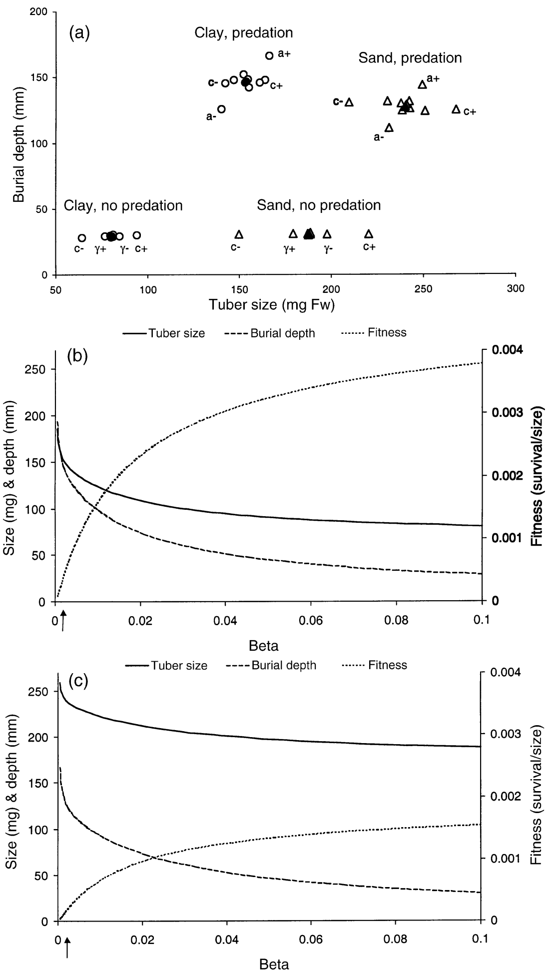

Fig. 5 Results of an optimization model predicting the effect of tuber predation on the tuber size and burial depth that maximize the number of surviving tubers per g dry-weight invested in their construction. (a) Main results and sensitivity analysis. Empty symbols represent the effect of 5% increments in the model parameters, letters indicate parameters in which 5% increments resulted in > 4% increments in the model output (tuber size or burial depth), + and – symbols indicate the direction of the 5% increments for a given point. (b) and (c) Effect on swan predation pressure (which increases with decreasing values of β) in clay-rich sediment and sandy sediment, respectively. Arrow indicates β-values in the field (β = 0.0017). Model parameters were a = 1.042; clay: c = 1.11, γ = 0.0087, b_1 = 0.0022, $b_2 = 21 \times 10^{-7}$; sand: c = 1.14, γ = 0.0036, b_1 = 0.00078, $b_2 = 56 \times 10^{-7}$.

Changing the value of β in simulations resulted in an increase in optimal tuber size (s^*) and optimal burial depth (d^*) with increasing predation pressure (i.e. as β decreases Fig. 5b, c). In clay-rich sediment (Fig. 5b) optimal tuber size was less variable than burial depth. At low predation pressures (β ≈ 0.1), an identical increase in predation pressure resulted in fourfold larger increases in d^* than in s^*. With increasing predation pressure, the increase in s^* grew larger until it became comparable with the increase in d^* at $\beta < 0.001$. In sandy sediment, s^* was always very large (190 mg fw for $\beta = 0.1$) and it increased much less than d^* with increasing predation pressure. Variation caused by comparable increments of β ranged from threefold larger in d^* than in s^* at the lowest predation pressure ($\beta \approx 0.1$) to ninefold larger at the highest predation pressure ($\beta = 0.0005$).

Figure 5(a) shows the results of a sensitivity analysis. Substantial changes (± 5%) in the parameter values had no effect on the general pattern of the results. In all cases: the fitness function had a global maximum; the optimal tuber size was larger for sandy than clay-rich sediments; and swan foraging led to an increase in optimal burial depth and an associated (though less pronounced) increase in optimal tuber size. The parameters that had the largest effect on the prediction are *a* and *c*. An increase in *a* leads to a downward shift in the 'swan-predation' survival curve $f(d)$ (i.e. an increase in swan predation) and the optimal response for the plant is to increase both burial depth and tuber size (cf. Ward & Saltz 1994). The parameter *c* is related to the intercept of the 'sprouting' survival curve $g(s,d)$: higher values of *c* are associated with the lower survival probabilities of small tubers, suggesting that plants will benefit from an increase in tuber size.

CLONAL VARIATION IN TUBER SIZE (COMMON-GARDEN EXPERIMENT)

Production ranged from 1 to 86 tubers and from 9 to 3008 mg dry-weight per plant (individual tubers ranged from 0.2 to 286 mg). Newly produced tubers showed a negative skewed size distribution within each plant (similar to tubers collected in the field; see also van Eerden *et al.* 1997). Average tuber size varied considerably between individual plants ($P < 0.001$, one-way ANOVA). Among-plant variation in tuber size was strongly correlated with initial tuber size ($P < 0.0001$, $r^2 = 0.33$, log-log linear regression of average tuber size on initial tuber size).

Initial tuber size, which did not vary between sites (Table 5), had a highly significant effect as a covariable in all two-way ANOVAS. Biomass and its allocation were significantly affected by site × treatment and by site, respectively (Table 5), although neither total tuber production nor the number of tubers per plant varied significantly. Tuber size was affected by site and by its interaction with field treatments (Table 5).

The path analysis indicated the existence of direct effects of initial tuber size on vegetative plant biomass and biomass allocation (Fig. 6) and these combined to explain 91% of the variation in tuber production, with initial tuber size having no further (i.e. direct) effect on production (Fig. 6). Higher tuber production was due to both more and larger tubers (Fig. 7a), but relative allocation to tuber size and number was not influenced by initial tuber size (direct effects were non-significant), and depended only on an internal trade-off (Fig. 6). Thus, although larger tubers tend to produce larger plants, which in turn produce more and larger tubers, there is considerable clonal variation in the allocation of a given amount of tuber production into many small or few large tubers.

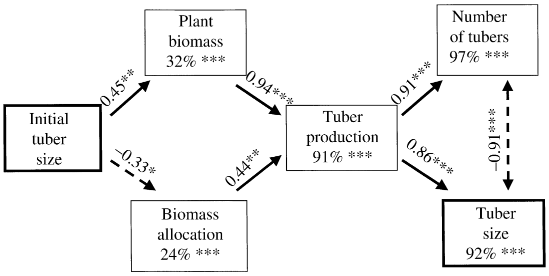

Fig. 6 Results of the path analysis: full lines indicate significant positive and dashed lines significant negative correlations. Partial correlation coefficients, together with their significance level, are indicated on arrows and coefficients of determination (percentage of explained variation), together with the significance level of the multiple regression, within boxes.

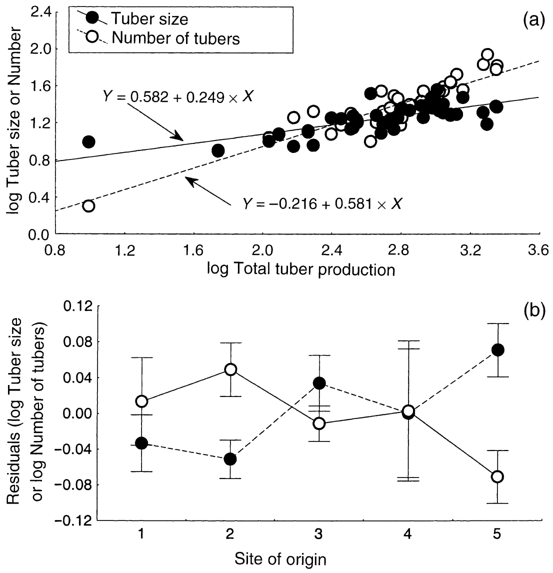

Fig. 7 Individual variation in tuber size (in mg dry weight) and the number of tubers produced by plants originating from 'mother' tubers collected at five different sites in the Babbelaar and grown in a common-garden experiment. (a) Linear regressions of tuber size and number, on total tuber production. (b) Effect of site of origin of the 'mother tuber' on tuber size and number, after correcting for the effect of total tuber production by using the residuals of the linear regressions shown in (a).

A two-way ANOVA in which total tuber production was entered as a covariable resulted in significant site effects on tuber size but not on tuber number (Table 5). After removing the effect of total tuber production by using the residuals of a double-log regression, plants from sites 1 and 2 (clay-rich and intermediate) had smaller tubers than those from sites 3, 4 and 5 (sandy; Fig. 7b). Although tuber number showed the reverse trend, it did not vary significantly among sites.

Table 5 Effect of site of origin and field treatment (grazed versus exclosed areas) on biomass and tuber production of *P. pectinatus* in common-garden conditions

		d.f.	F	P	r^2
Variable					
Initial tuber size (dw)*	Site	4	0.77	0.55	–
	Treatment	1	0.04	0.84	–
	Site × treatment	4	0.85	0.51	–
	Error	32	–	–	–
*Covariable: initial tuber size (dw)**					
Vegetative biomass (dw)	Site	4	0.44	0.78	–
	Treatment	1	0.36	0.55	–
	Site × treatment	4	3.72	**0.014**	–
	Error	31	–	–	–
	Covariable	1	30.78	**0.000004**	0.50
Shoot : root ratio*	Site	4	5.67	**0.0015**	–
	Treatment	1	3.05	0.091	–
	Site × treatment	4	1.26	0.31	–
	Error	31	–	–	–
	Covariable	1	12.97	**0.0011**	0.29
Tuber production (dw)	Site	4	1.25	0.31	–
	Treatment	1	0.27	0.60	–
	Site × treatment	4	2.59	0.056	–
	Error	31	–	–	–
	Covariable	1	30.80	**0.000004**	0.50
Number of tubers per plant	Site	4	1.17	0.34	–
	Treatment	1	0.11	0.75	–
	Site × treatment	4	1.22	0.32	–
	Error	31	–	–	–
	Covariable	1	15.26	**0.00047**	0.33
Average tuber size (dw)†	Site	4	2.76	**0.045**	–
	Treatment	1	0.24	0.63	–
	Site × treatment	4	3.88	**0.011**	–
	Error	31	–	–	–
	Covariable	1	18.78	**0.00014**	0.38
Covariable: total tuber production (dw)					
Number of tubers per plant	Site	4	1.38	0.26	–
	Treatment	1	0.05	0.81	–
	Site × treatment	4	0.83	0.51	–
	Error	31	–	–	–
	Covariable	1	179.7	**0.000001**	0.85
Average tuber size (dw)†	Site	4	2.70	**0.049**	–
	Treatment	1	1.17	0.29	–
	Site × treatment	4	1.28	0.30	–
	Error	31	–	–	–
	Covariable*	1	31.12	**0.000004**	0.50

Significant effects ($P < 0.05$) are printed in bold; marginally significant effects ($P < 0.10$) are underlined. *Log-transformed. †Log-transformed before averaging (original data were strongly skewed).

Discussion

Deep sediment layers and clay-rich areas appear to act as refuges for sago pondweed tubers grazed upon by Bewick's swans. Swans reduced tuber biomass by 48% to a value (2–10 g dry weight m^{-2}) similar to the 'giving-up' threshold reported by Beekman *et al.* (1991) and van Eerden *et al.* (1997). However, the giving-up biomass may be spatially variable with swans foraging more intensively on sandy areas (Table 3) and in upper sediment layers (Fig. 3).

OPTIMAL TUBER SIZE AND PLANTING DEPTH

Average tuber size increased eightfold over the range of depths studied, so that, although tuber-bank density peaked at intermediate depths, biomass continued to increase with increasing depth (Fig. 2; see also Spencer 1987 and Beekman *et al.* 1991). Spencer (1987) proposed waterfowl herbivory and the risk of stochastic drought events as an explanation for the existence of this gradient despite the decrease in spring survival (sprout emergence) associated with increasing depth. Drought events do not occur in the Babbelaar and ice scouring of the sediment surface is also rare. Although winter storms could wash out tubers in the upper sediment layers, our data show no such effect of depth on winter mortality. Grazing by Bewick's swans is therefore probably the main source of depth-dependent mortality. Horizontal variation in predation pressure (associated with varying sediment composition) also led to differences in the relationship between survival and burial depth (Table 3). As sprout emergence (which decreased with burial depth but increased with tuber size) was lower in sandy sediment, comparable survival at a given depth requires larger tubers (i.e. increased construction costs) than in clay-rich areas. Increases in mortality and construction costs are thus likely to constrain the beneficial effect (in terms of reduced predation) of deeper burial, particularly in sandy areas, where predation pressure is also higher (see also Nolet *et al.* 2001).

Horizontal variation in predation pressure at our sites was similar in 1996 and 1997 although tuber production varied (41 and 33 g dry weight m^{-2}, respectively; Nolet *et al.* 2001). This might be expected to result in selection pressure favouring (or having favoured in the past) those genets which produce 'optimal' tuber sizes and planting depths at a given site (i.e. those that maximize survival). In the absence of swan predation, small tubers placed close to the surface would be optimal, as seen at the clay-rich site 1 (data not shown). Moderate to high predation pressures result in a severe increase in mortality with decreasing burial depth, favouring large tubers deep in the sediment as reflected in model results at reduced values of β, particularly in sandy sites (Fig. 5). The differences observed among field sites could, however, also result from factors not included in our analysis (e.g. differences in rhizome penetration between clay-rich and sandy sediment).

INDIVIDUAL VARIATION IN TUBER SIZE

The preferential use of spatial refuges (greater burial depths) by the plants requires tuber depth and size characteristics to be consistent across generations, i.e. large, deep tubers should produce relatively larger, deeper tubers in the following growth season. This can be achieved in two different, though not mutually exclusive, ways: through genetical effects (clonal differentiation, which requires the existence of heritable individual variation in tuber size, onto which the selection pressure could act) or through environmentally induced carry-over effects (often referred to as non-genetical 'maternal effects'; Huber *et al.* 1996; Rossiter 1996).

We chose to focus on tuber size, based on the strong correlation between burial depth and tuber size (in particular, large tubers were never found in the field at the uppermost sediment layers). Although, when cultivated under identical conditions, plants originating from large tubers tended to produce larger tubers (an effect mediated by higher tuber production; Fig. 6), we could not partition environmentally induced and genetical components. The path and covariance analyses, however, indicate an indirect correlation between initial and 'offspring' tuber size (detailed in Fig. 6), which is most easily explained by carry-over effects, whereby larger resource availability in the initial tuber results in higher (plant and tuber) biomass yield and thus larger tubers. The absence of direct correlations between initial and 'offspring' tuber sizes suggest that there are no direct maternal effects (unless they were masked by genetic correlations, e.g. for a given initial tuber size, plants producing larger tubers have a lower biomass yield).

On the other hand, significant differences in the size-number trade-off between sites (Fig. 7b) most likely indicate clonal differentiation. These differences are independent of total tuber production (they were significant after entering tuber production as a covariable; Table 5) and they were not affected by plant size, biomass allocation and initial tuber size (these variables were not directly correlated with tuber size or number; Fig. 6). Although carry-over effects that were not mediated by initial tuber size (e.g. increased tuber reserves due to higher nutrient supply during the previous growth season) provide an alternative explanation, tubers from nutrient-poor (sandy) sites produced larger rather than smaller tubers.

Both non-genetical maternal effects (large tubers make larger plants and thus larger tubers) and clonal differentiation (differences in size-number allocation resulting from local adaptation or from stochastic genetic variation), therefore, contribute to the vertical distribution of pondweed tubers subject to swan predation.

INTERACTION WITH VEGETATIVE GROWTH

Our analysis considered only the effects of three sources of mortality (predation by Bewick's swans, death during winter dormancy due to soil pathogens and parasites and failure of emergence) on the optimal size and burial depth of pondweed tubers. We excluded any effects that intrinsic or environmental factors acting during the summer (i.e. the growing season) may have on pondweed population dynamics. Growth rate tends to increase with tuber size following a logistic or hyperbolic function, and the resulting effects on fitness may cause deviations from the optimization model.

The existence within populations of propagule size 'strategies' that optimize either colonization or competition is currently under intensive debate (McGinley *et al.* 1987; Weiner 1988; Venable 1992; Geritz 1995; Cheplick 1996; Declavijo & Jimenez 1998; Geritz *et al.* 1999). In pseudo-annuals, larger tubers should generally have an advantage in densely populated situations because their higher growth rates give them a competitive advantage (Spencer & Ksander 1991), whereas smaller tubers are not better colonizers (Verburg & During 1998; see also Geritz 1995; Geritz *et al.* 1999). In our case, however, swans reduce the tuber-bank densities every year and competitive interactions are therefore probably less important than tuber mortality in regulating clonal selection (H.H. Hangelbroek, unpublished data).

CONSEQUENCES FOR THE SWAN–PONDWEED INTERACTION

When considering the interactions between herbivores and plant propagules, such as between Bewick's swans and *P. pectinatus* tubers (Beekman *et al.* 1991; van Eerden *et al.* 1997), active, choice-making foragers are often assumed to act on passive, unresponding prey populations. Some plant–consumer interactions are, however, two-sided: here, selection in intensively grazed areas for large, deeply buried, tubers is likely to lead to less accessible food one year/generation later, and the resulting reduced predation pressure will then favour shallower, more accessible tubers (see also Ward & Saltz 1994). Whether this feedback mechanism brings stability to the relationship, results in fluctuating variation in predation pressure, or is irrelevant at the scale at which swan foraging takes place, will depend both on the spatial variation in sediment characteristics and the scale at which foraging swans perceive and exploit their environment. The study of foraging strategies followed by propagule-eating herbivores should, however, include effects of foraging on propagule availability, as such feedbacks are likely to constrain the effect of the herbivore on the plant population and could also have large effects on plant persistence.

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