

Cascading effects of variation in plant vigour on the relative performance of insect herbivores and their parasitoids

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Abstract. 1. Consequences of variation in food plant quality were estimated for a system consisting of two monophagous noctuid herbivores and three ichneumonid parasitoids.

2. In a natural population, pupal weights of the herbivores in this system, *Nonagria typhae* and *Archanara sparganii*, were found to be highly variable. Pupal weights increased strongly and consistently with the increase in the vigour of the host plant, *Typha latifolia*, providing support for the plant vigour hypothesis. Correspondingly, as the moths do not feed as adults, a strong, positive correlation between host vigour and fecundity of the herbivores would be expected.

3. There were strong and positive relationships between adult body sizes of the parasitoids and the sizes of their lepidopteran hosts. Moreover, a direct, positive link between plant quality and parasitoid size was documented.

4. For all three parasitoids, cascading effects of plant quality on body size were weaker than for the herbivores. Differences in the importance of adult feeding and oviposition behaviour suggest that dependence of fitness on body size is also weaker in the parasitoids than in the moths. It is therefore concluded that the numerical response of the herbivore population to a change in plant quality should exceed the corresponding response in the parasitoids.

5. The results of this work imply that variation in plant variables may affect performance of different trophic levels to a different extent. It is suggested that the importance of adult feeding for the reproductive success (capital vs. income breeding strategies) in both herbivores and parasitoids is an essential aspect to consider when predicting responses of such a system to changes in plant quality.

Key words. Adult feeding, *Archanara*, body size, cascading effects, Ichneumonidae, *Nonagria*, population dynamics, *Typha latifolia*.

Introduction

Trophic cascades can be defined as strong interactions within food webs that influence system properties and embrace at least two trophic links (Pace *et al.*, 1999). Both bottom-up and top-down trophic cascades may influence community-level processes and population dynamics of single species (Polis & Strong, 1996; Polis *et al.*, 2000;

Sinclair *et al.*, 2000). In terrestrial ecosystems, one of the most universal bottom-up cascades is based on plants (Price, 1992). In particular, heterogeneity in food plant quality has a strong potential to affect body size in herbivorous insects (Hunter & Price, 1992; Price, 1992). In turn, body size of an adult insect is frequently a good predictor of life-history parameters (e.g. fecundity, longevity, and survival) that have direct relevance to population dynamics (Honěk, 1993; Nylin & Gotthard, 1998; but see Leather, 1988). Most data on the effects of plant quality on insect performance come from laboratory studies, however less is known about the range of food plant-induced size variation

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in natural herbivore populations (e.g. Roland & Myers, 1987; Kaitaniemi *et al.*, 1999). Moreover, the question of whether vigorous or stressed plants provide a more favourable food source for insect herbivores remains controversial (Koricheva *et al.*, 1998). While manipulative studies are necessary to reveal causal connections, correlative analyses assessing the scope of the effects in the field are of no less importance.

Cascading effects of variation in plant resources may extend to the performance of the third trophic level, parasitoids and predators (Price *et al.*, 1980; Duffey *et al.*, 1986; Faeth, 1994; Turlings & Benrey, 1998). Among these, parasitoids are expected to be particularly sensitive to variation in the quality of their insect hosts because of their tight developmental coupling with host insects. This is supported by numerous laboratory studies that have shown the influence of host diets on parasitoid development and body size (Bloem & Duffey, 1990; Barbosa *et al.*, 1991; Bourchier, 1991; Werren *et al.*, 1992). The effect of host diet on body size of insect parasitoids is commonly mediated by host size (e.g. Pettitt & Wietlisbach, 1993; Heinz, 1996; Teder *et al.*, 1999), however there is a limited amount of information on the range of host- and plant-quality-dependent variations in parasitoid body size in natural populations. Moreover, little is known about which of the two counterparts, the host or the parasitoid, is affected more strongly by changes in plant quality. This question becomes important when considering the dynamics of a host–parasitoid system: an increase or decrease in plant quality may affect host and parasitoid numbers to a different extent.

The work reported here on natural populations documents a strong, positive correlation between pupal weight of lepidopteran herbivores and vigour of their host plant, *Typha latifolia*. Further, it is shown that parasitoid body size depends on the pupal weight of the herbivore and, directly, on the characteristics of the plant. The relative strength of plant quality effects on herbivore and parasitoid fitness and population dynamics is discussed considering their adult feeding strategies.

Materials and methods

Study area and organisms

The study examining tritrophic interactions in a natural plant–herbivore–parasitoid system was conducted from 1995 to 1998 near Tartu, south-eastern Estonia (58°22'N, 26°45'E). Study areas were located on the flooded meadow of the Emajõgi river where water usually recedes by the end of May. In order to assess the effects of both temporal and spatial variation in plant characteristics on insect performance, two habitats somewhat different with respect to homogeneity of growth conditions and abundance of a cattail, *Typha latifolia* L. (Typhaceae), were examined. The habitat studied in 1995–1996 was characterised by quite homogeneous vegetation, with *T. latifolia* dominant. Other plant species, *Solanum dulcamara* L., *Cicuta virosa* L., *Glyceria maxima* Hartm., *G. fluitans* L., *Carex elata* Bell. ex

All., and *Epilobium palustre* L., were common but formed a minor part of the plant cover. In 1997–1998, a more heterogeneous habitat with patches of *T. latifolia* and *C. elata* alternating was examined. The two study areas were separated by a distance of ≈ 300 m.

The study system was based on *T. latifolia*, a rhizomatous perennial helophyte (i.e. a plant growing in soil saturated with water) forming dense stands up to 3 m in height. The larvae of four moth species were found to feed on leaves and stems of *T. latifolia*, however the study was restricted to the two most abundant species, *Nonagria typhae* Thunb. and *Archanara sparganii* Esp. (Lepidoptera: Noctuidae), the other species being too scarce to allow a meaningful analysis (<1% of all larvae). The phenology and feeding biology of these two taxonomically close univoltine species are similar. They overwinter as eggs that hatch in spring. Larvae feed on the aerial roots of the host plant at the beginning of the season, switching to endophytic feeding on the shoots later (Galichet *et al.*, 1992). One individual therefore usually feeds on more than one shoot during the larval period. Larvae of *N. typhae* are reported to be monophagous on *T. latifolia* while larvae of *A. sparganii* may also use some other species (Skou, 1991), however in the studied areas, both species were apparently functionally monophagous on *T. latifolia*. At the end of July or the beginning of August, larvae pupate inside the shoot or between the leaves of the host plant. The pupal period lasts for about a month in both species. Because adults of both *N. typhae* and *A. sparganii* do not feed, the potential fecundity of the females of these species should be determined largely by their weight at eclosion.

Three principal species of solitary parasitoid were found to parasitise larvae and pupae of *N. typhae* and *A. sparganii*: *Exephanes occupator* Grav., *Spilichneumon limnophilus* Thoms., and *Chasmodon paludator* Desv. (Hymenoptera: Ichneumonidae). Other parasitoids accounted for <1% of total parasitism. Like their hosts, studied parasitoids have univoltine life cycles. Adult females overwinter and lay their eggs on young moth larvae in late spring (*E. occupator*; T. Teder, pers. obs.; and probably also *S. limnophilus*) or on pupae in July and August (*Ch. paludator*; Hinz, 1983). Adult wasps emerge from moth pupae more or less simultaneously with unparasitised moths. All three parasitoids are oligophagous and are also known to parasitise some other moths (Rasnitsyn & Siitan, 1981), which, however, apparently constitute only a minor fraction of hosts in the studied system. All three parasitoids show a preference for *N. typhae*, the larger of the two host species (Teder *et al.*, 1999).

Sampling and measurements

Field populations were sampled to obtain data on the extent of natural variation in plant vigour, as well as body sizes of moths and parasitoids. Sampling was conducted at the end of July and/or beginning of August in 4 consecutive years (1995–98). Each year, 20–33 plots of $\approx 2 \times 2$ m, 3×3 m, or 4×4 m (depending on larval abundance in the particular

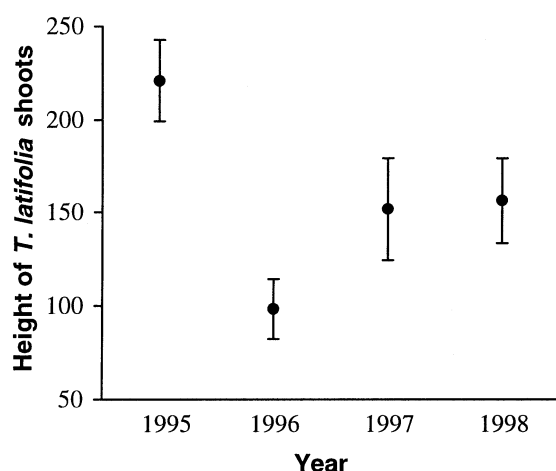


Fig. 1. Among-year variation in the height of *Typha latifolia* shoots. Error bars indicate SD.

year) were sampled. In the area with the homogeneous habitat, plots were selected systematically along transects at 20 m intervals in an area of $\approx 300 \times 100$ m. In the area with the heterogeneous habitat, $\approx 200 \times 200$ m in size, plots were selected so as to obtain samples from patches with variable heights of *T. latifolia*. As indices of plant vigour, the total number of live shoots on each plot, the proportion of generative shoots (in 1997), and a height index of *T. latifolia* were recorded for every plot. This was done simultaneously with insect collections. To eliminate the influence of outlying plant individuals, the height index was obtained by measuring the height of about the 15th highest vegetative shoot in the plot. Using such a simple method was justified by the limited within-plot variation in the height of the shoots, which was exceeded considerably by the variation among plots and years (Fig. 1). Moreover, the height index used correlated strongly and positively with two other indices of vigour: plant biomass and proportion of generative shoots (Fig. 2, see also Results). Moth pupae were collected from the study plots by inspecting all the cattail shoots carefully. The pupae were relatively large (2.0–3.5 cm in length), potential pupation sites were limited, and damaged shoots were easily distinguishable from undamaged shoots, so it was possible to collect nearly all pupae from the plots. The number of pupae collected each year varied from 1022 to 2684, the average number of pupae per study plot being 45. Pupae were stored in Petri dishes until eclosion of the adult moth or parasitoid.

Weight of live pupae was used as an index of the moths' body size. Weight of parasitoids was determined in two ways. In 1997 and 1998, dry weight of adult parasitoids was measured. Comparable weight indices of parasitoids originating from 1995 and 1996 could not be obtained in a similar way because, in these years, the emerged parasitoids had not been weighed in the year of collection, and different conditions of preservation had apparently affected their weights. Estimates of dry weight for these parasitoids were therefore calculated using the regression of weight of parasitised pupae on dry weight of corresponding adult

parasitoids in 1997 (*E. occupator* females: $R^2 = 0.47$, males: $R^2 = 0.59$; *S. limnophilus* females: $R^2 = 0.55$, males: $R^2 = 0.72$; *Ch. paludator* females: $R^2 = 0.27$, males: $R^2 = 0.26$). Such a method could be used as the parasitoid pupae embraced a considerable proportion of the volume of host pupae. Furthermore, the applicability of this transformation was confirmed by measuring the hind tibia length of a sample of emerged parasitoids: in all parasitoid species, there was a positive relationship between the weight of parasitised pupae and this linear measure of body size ($P < 0.001$ for all species), and the slopes did not differ between years with different host quality (ANCOVA: $P = \text{NS}$ for all year \times pupal weight interaction terms, average sample size = 65 per species). A representative sample of moths was used for estimating fecundity as a function of body

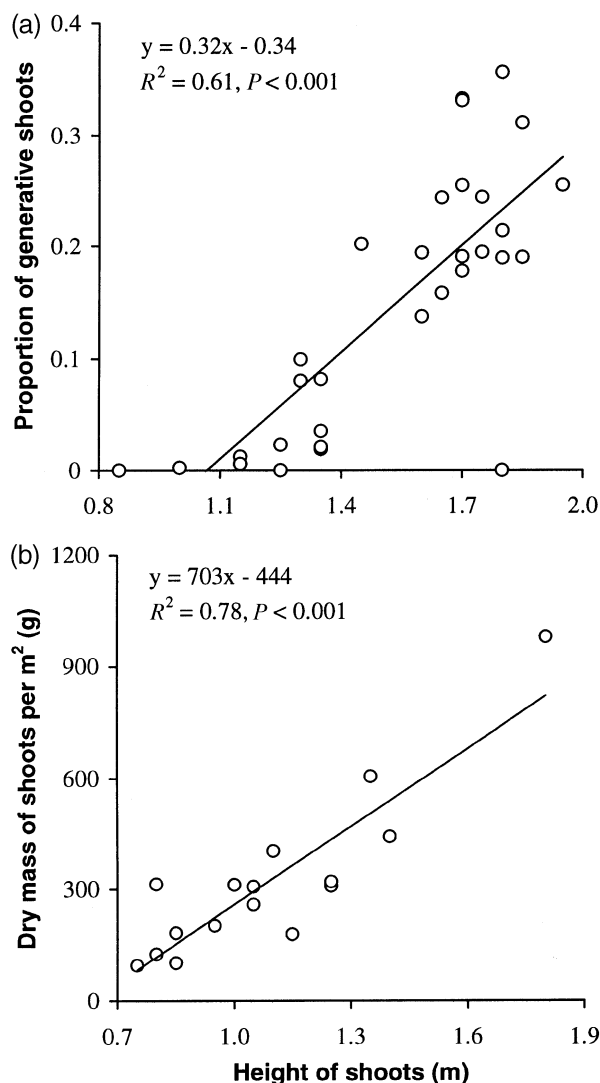


Fig. 2. (a) The relationship between height of *Typha latifolia* shoots and proportion of generative shoots in plots in 1997 and (b) the relationship between height of *T. latifolia* shoots and their dry biomass per m² (samples were taken from the studied stand in 1997).

size. For this purpose, eclosed female moths were kept in Petri dishes until they died, their abdomens were then dissected, and chorionated eggs were counted.

Data analysis

The levels of natural variation in plant performance and insect body sizes, and the relationships between them, were studied by two complementary approaches. First, patterns of temporal variation were studied on the basis of yearly means. Second, high variance in plant vigour in 1997 allowed analysis based on spatial variation.

In the within-year analyses, plot-specific averages of respective variables (e.g. average pupal weight of *N. typhae* males collected from one plot) were used as independent observations in regressions. In the among-year comparisons, the regressions were based on mean values of plot averages in study years. Weights of parasitoids were corrected for sex using a linear regression of plot means, and, thereafter, sexes were pooled to increase sample sizes in corresponding analyses. The analyses examining herbivore–parasitoid relationships were based on the most numerous herbivore of the system, *N. typhae*, and its parasitoids. The number of parasitoids that emerged from *A. sparganii* was too low for the analyses.

The relationship between pupal weights of moths and corresponding adult weights of parasitoids was estimated at the level of plot means to compare the relative sensitivity of moths and parasitoids to environmental variation in the studied plots. As both variables contained random variation, type I regression was an inappropriate technique to derive a functional relationship, so type II regression had to be used (Sokal & Rohlf, 1995; see also e.g. Fairbairn, 1997). The type II regression was performed by calculating the first principal component (PRINCOMP procedure; SAS Institute Inc., 1995). This line is fitted by finding the minimum of the sum of squared deviances from the regression line, measured perpendicular to the line. Prior to the analyses, weights of studied parasitoids and moths were standardised by dividing them by species- and sex-specific means.

To compare the effects of *T. latifolia* vigour on sizes of moths and parasitoids directly, a corresponding ANOVA design (MIXED procedure; SAS Institute Inc., 1995) was applied to the 1997 within-year data. Species, sex, and plot were used as classification variables. The model contained weight as the dependent variable and species (moth, parasitoid), sex (male, female), height of shoots, and two interaction terms (species \times height of shoots, species \times sex) as independent effects. The interaction term plot \times species was treated as a random effect.

Results

Variation in the vigour of *Typha latifolia*

There was considerable among-year variation in performance in the studied stands of *T. latifolia*. The average

height of vegetative shoots ranged from 1.0 m in 1996 to 2.2 m in 1995 (Fig. 1). Spatial variation within the study area was highest in 1997, when the height in the study plots ranged from 0.85 to 1.85 m (average \pm SD = 1.52 ± 0.28 m), with the variation being notably lower in other years. The height of shoots correlated positively with another variable related to plant performance, proportion of generative shoots (Fig. 2a), which also showed considerable plot-to-plot variation (0–36%) in 1997. In addition, the height of shoots was a good indicator of the above-ground biomass per unit area (Fig. 2b). Height of shoots can thus be considered an uncontroversial measure of vigour in *T. latifolia*.

Water conditions, highly variable both spatially and among years, formed an obvious factor responsible for observed variation in *T. latifolia*: the performance of plants was clearly poorest in the dry year 1996, when the stand was not flooded in spring. Similarly, the high within-year variation in 1997 was apparently related to variable water conditions in the study area.

Variation in the body size of the moths

The studied herbivores, the moths *N. typhae* and *A. sparganii*, showed a high level of variation in body size, with notable differences in moth pupal weights among years (ANOVA: *N. typhae* females: $F=43.3$, d.f. = 3, $P<0.001$; males: $F=27.0$, d.f. = 3, $P<0.001$; *A. sparganii* females: $F=7.2$, d.f. = 3, $P<0.001$; males: $F=1.2$, d.f. = 3, $P=NS$). In 1995, females of *N. typhae* were 1.3 times heavier and females of *A. sparganii* 1.2 times heavier on average than in 1996. In 1997 and 1998, moths were of intermediate size (Fig. 3). There was about a 3.2-fold weight difference between the smallest and largest females of *N. typhae* in 1997 (average \pm SD = 0.83 ± 0.15 g), when spatial variation in the system was the highest. For female *A. sparganii*, the corresponding difference was 2.4-fold (average \pm SD = 0.44 ± 0.07 g). The range of variation for males was of similar magnitude. Significant differences were also detected consistently in average moth sizes at the level of studied plots: the smallest and largest plot averages for females of *N. typhae* and *A. sparganii* differed 1.9 and 1.7 times respectively (Fig. 4).

Relationships between plant performance and moth size

Among years, the correlations between height of shoots and pupal weight of moths were all strongly positive with the exception of male *A. sparganii* (Fig. 3). Within-year comparisons confirmed the among-year results: in 1997, when variation in performance of *T. latifolia* among patches was highest, there was a significant, positive association between height of *T. latifolia* and pupal weight for both sexes of *N. typhae* and for female *A. sparganii* (Fig. 4). Once again, however, the pupal weight of male *A. sparganii* did not depend on the height of shoots (Fig. 4). These trends were similar for the proportion

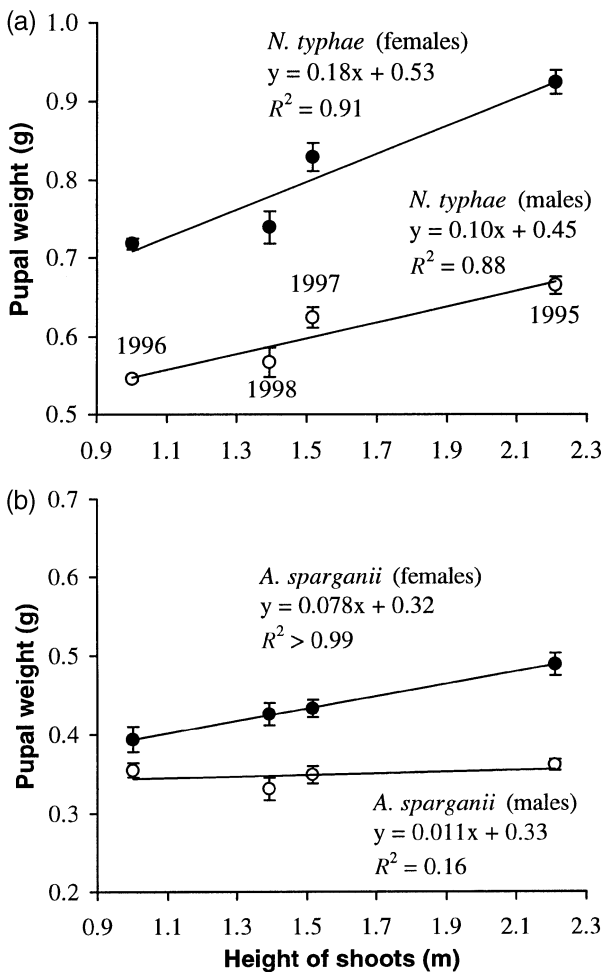


Fig. 3. Among-year relationships between height of *Typha latifolia* shoots and pupal weight of the herbivores (a) *Nonagria typhae* and (b) *Archanara sparganii*. Each point represents the mean value of plot averages in 1 year. Error bars indicate SE. Statistics are for type I regression.

of generative shoots (*N. typhae* females: $R^2 = 0.34$, $P < 0.001$, males: $R^2 = 0.38$, $P < 0.001$; *A. sparganii*, females: $R^2 = 0.22$, $P < 0.05$, males: $R^2 = 0.01$, $P = \text{NS}$). In other years, within-year variation in food plant performance was lower. Still the associations between pupal weights and height of shoots were all positive though not significant.

Effect of host size on parasitoid size

Within-year comparisons in 1997 showed positive relationships between pupal weights of *N. typhae* and weights of its parasitoids: larger parasitoids came from plots with larger *N. typhae* (Fig. 5a–c). The association was significant for *E. occupator* and *Ch. paludator* but not for *S. limnophilus*. Similar results were obtained when year averages were compared: in years with larger hosts, all three parasitoids achieved a larger size on average (Fig. 6a–c). Differences among years

in body size were significant in male *E. occupator* (ANOVA: $F = 5.41$, d.f. = 3, $P < 0.01$), female *Ch. paludator* ($F = 7.83$, d.f. = 2, $P = 0.001$), and *S. limnophilus* ($F = 3.53$, d.f. = 3, $P < 0.05$), and almost significant in females of *E. occupator* ($F = 2.65$, d.f. = 3, $P = 0.053$). These results are in good agreement with those of an earlier study of the system (Teder *et al.*, 1999), which demonstrated that parasitoids emerging from *N. typhae* were larger on average than those that developed on the smaller host species, *A. sparganii*. Moreover, while female *N. typhae* were larger than males by $\approx 30\%$, parasitoids emerging from females attained larger sizes than those that developed from males (Teder *et al.*, 1999).

Effect of plant vigour on parasitoid size

Variation in the height of *T. latifolia* had a substantial influence on the adult size of parasitoids (presumably mediated by host size). Within-year comparisons showed

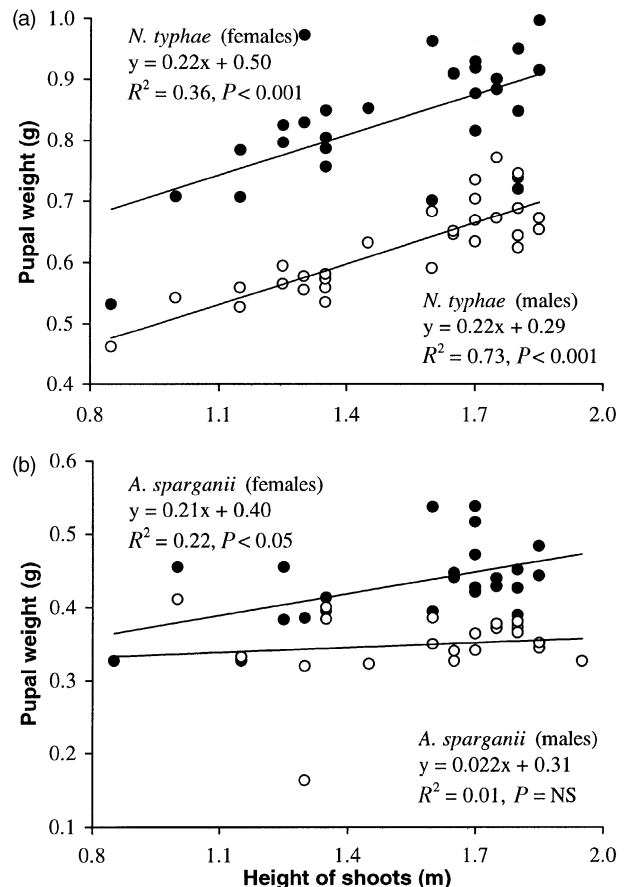


Fig. 4. Within-year (1997) relationships between height of *Typha latifolia* shoots and average pupal weight of (a) *Nonagria typhae* and (b) *Archanara sparganii*. Each point represents one study plot. Statistics are for type I regression.

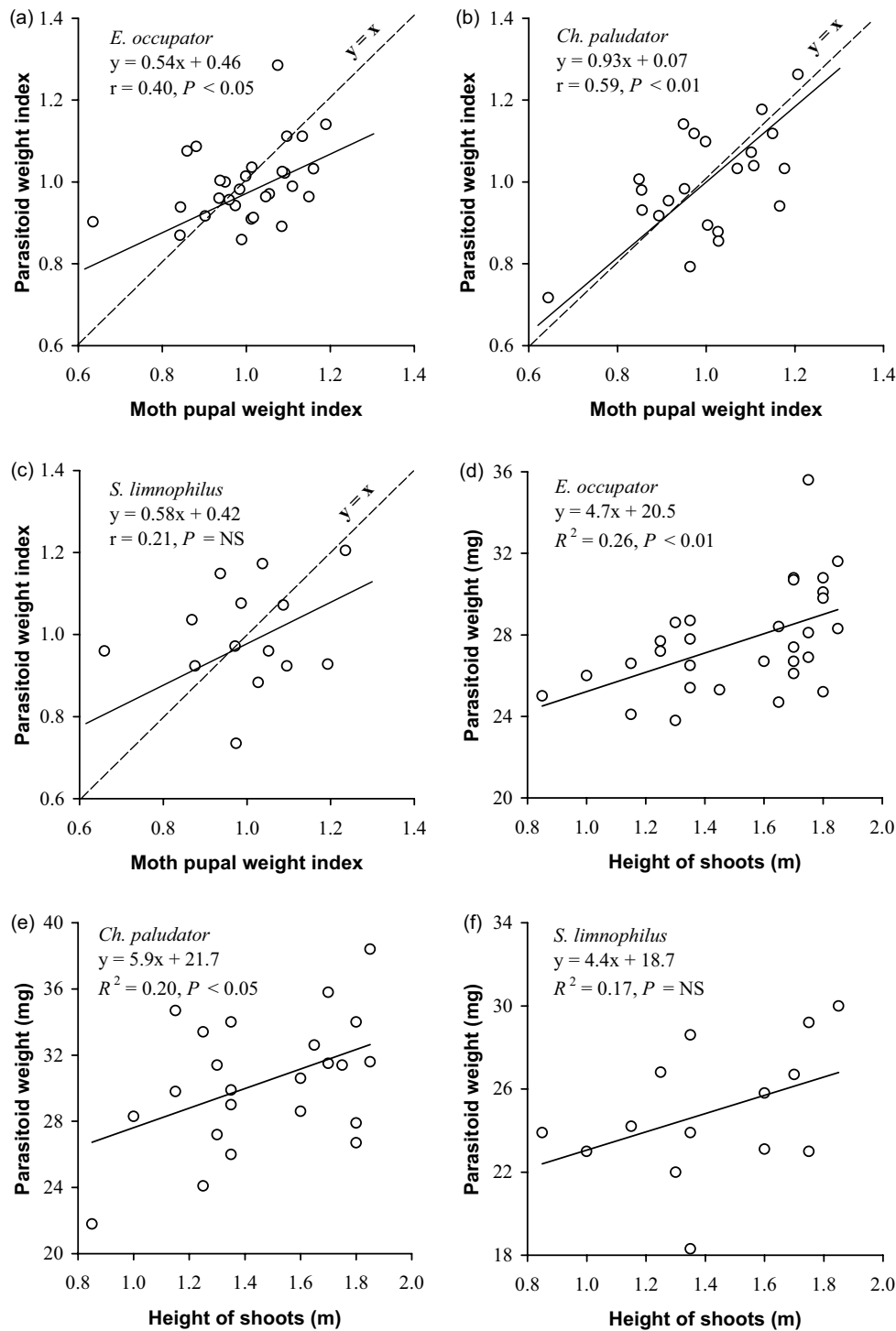


Fig. 5. (a–c) Within-year (1997) relationships between pupal weight of *Nonagria typhae* and dry adult weight of studied parasitoids. Pupal weight and parasitoid weight are expressed in relation to the overall mean of the respective variables. The solid lines and equations correspond to type II regressions. r and P values are those of Pearson correlations. The dashed lines presented for reference would correspond to equal relative increase in weights with environmental conditions improving. (d–f) Within-year relationships between height of *Typha latifolia* shoots and dry adult weight of studied parasitoids. Statistics and equations are for type I regression. Each point represents one study plot.

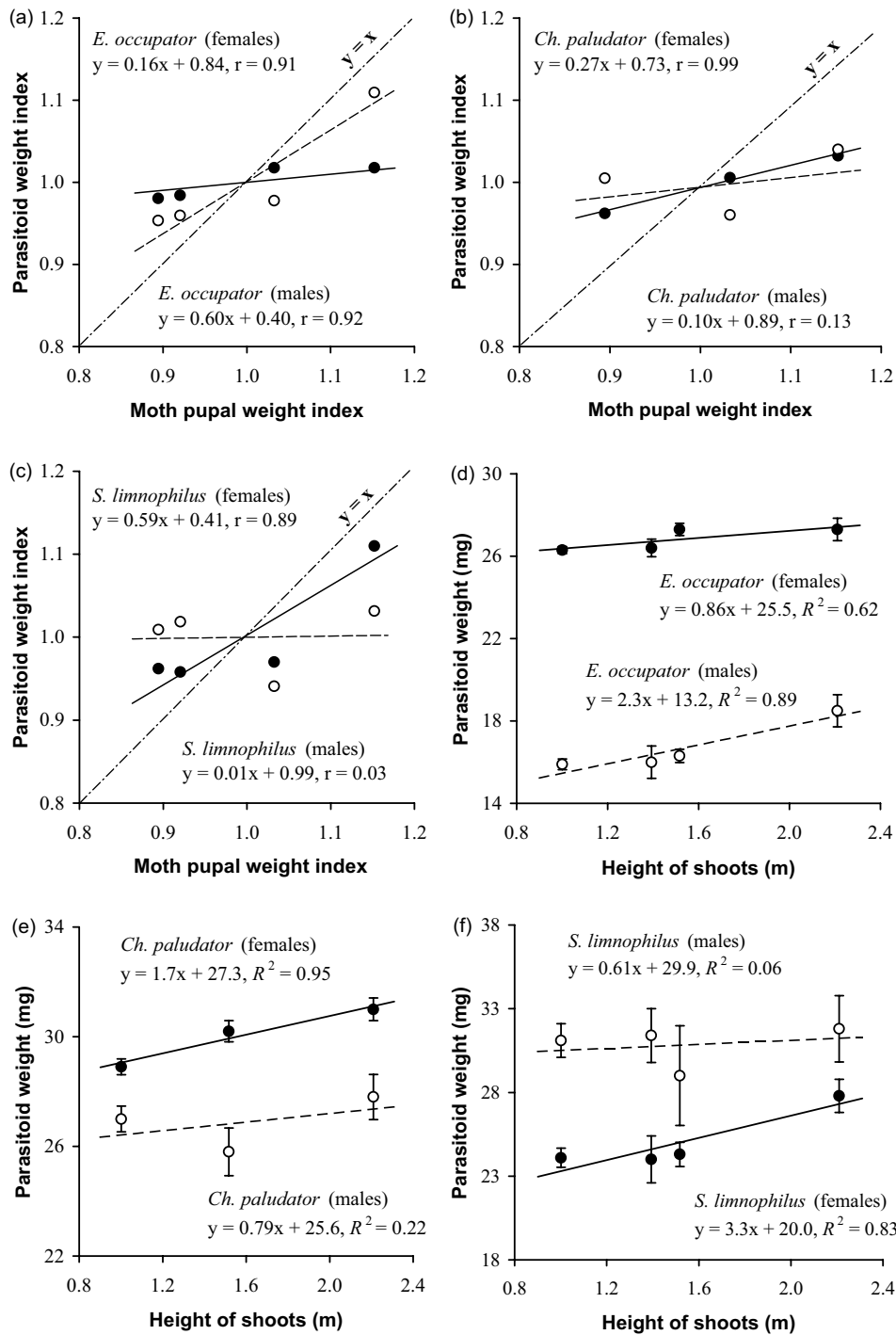


Fig. 6. (a–f) Among-year relationships between pupal weight of *Nonagria typhae* and dry adult weight of studied parasitoids. Each point indicates a mean value of plot averages in the respective year. Pupal weight and parasitoid weight are expressed in relation to the mean value of the study years. The solid (● females) and dashed (○ males) lines and equations correspond to type II regressions. r and P values are those of Pearson correlations. The diagonal lines (---) presented for reference would correspond to equal relative increase in weights with environmental conditions improving. (d–f) Among-year relationships between height of *Typha latifolia* shoots and dry adult weight of studied parasitoids. Statistics and equations are for type I regression. Each point represents 1 study year. Error bars indicate SE of plot means.

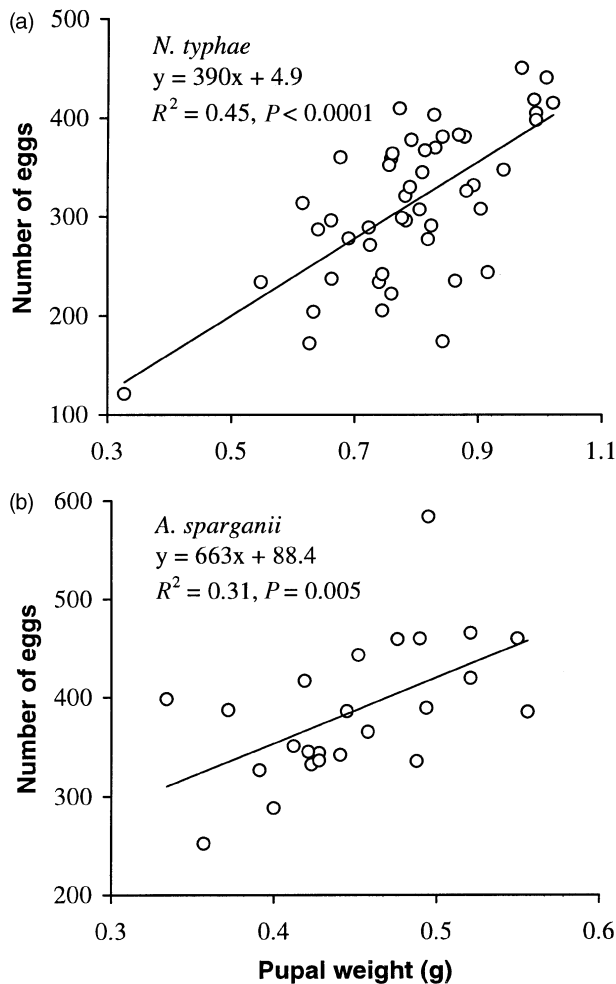


Fig. 7. Relationships between pupal weight and number of eggs in studied moths ($n=48$ for *Nonagria typhae*, $n=24$ for *Archanara sparganii*).

significant, positive associations between plant vigour and adult size of *E. occupator* (Fig. 5d) and *Ch. paludator* (Fig. 5e). A positive response to plant vigour was also observed in *S. limnophilus* but the association was not significant (Fig. 5f). Among-year comparisons gave similar results: both sexes of all three parasitoids showed a positive response to plant vigour, the associations being strongest in males and females of *E. occupator* and females of *Ch. paludator* and *S. limnophilus* (Fig. 6d–f).

Comparison of body size variation in moths and parasitoids

Indices of plant vigour (height of shoots and proportion of generative shoots) had a positive influence on the size of both moths and their parasitoids, however the slopes of all regression lines (type II) estimating the relationship between pupal weights of moths and adult weights of parasitoids showed values below unity (Figs 5a–c and 6a–c). This indicates a weaker relative response of parasitoids to

environmental variation across the study plots: e.g. a 10% increase in moth weight corresponded to less than a 10% increase in parasitoid weight. Within-year comparisons accorded well with among-year results (Figs 5a–c and 6a–c).

Additionally, an ANOVA was used (see Methods) to compare the effect of plant variation on moth and parasitoid body size directly. All the parasitoids consistently exhibited a weaker response to changes in plant quality than did *N. typhae* moths; the effect attained significance for the most numerous parasitoid, *E. occupator* (interaction between height of shoots and species: $t = -2.41$, d.f. = 646, $P < 0.05$).

Effect of body size on fecundity in moths and parasitoids

It was possible to assess potential fecundity in the studied moths but not in the parasitoids. In the moths collected as pupae in the field, body size and the number of eggs were correlated strongly and positively: a twofold difference in pupal weight caused a slightly less than twofold difference in the number of eggs (Fig. 7). Ovaries of studied parasitoids start developing after overwintering with the increase in temperature (Hinz, 1983). No eggs could therefore be found in the abdomens of females that emerged in the autumn. All three parasitoids are synovigenic: their eggs mature throughout adult lives.

Discussion

Performance of *T. latifolia*, both when measured as height of shoots and proportion of generative shoots, was found to vary widely both spatially and temporally. This is in accordance with earlier studies showing that performance of *T. latifolia* is sensitive to various environmental factors, e.g. shading (Grace & Wetzel, 1981) and water depth (Grace & Wetzel, 1982). The high variability in host plant quality induced strong cascading effects on performance of higher trophic levels – herbivores and parasitoids. The indices of food plant vigour and body sizes of studied moths were found to be correlated strongly and positively (Figs 3 and 4), thereby supporting the plant vigour hypothesis (Price, 1991). The influence of plant parameters was consistent both among years and among patches within a year. Moreover, the responses of the two herbivores were notably similar. It is thus concluded that host plant vigour represents a major and predictable determinant of moth performance in the studied system. A positive correlation between plant vigour and herbivore performance is, however, not ubiquitous (Mattson & Haack, 1987, and references therein). The strong, positive correlations observed in the present study can presumably be ascribed to the high growth rate of *T. latifolia* (Prach & Wade, 1992; T. Teder and T. Tammaru, pers. obs.). Fast-growing plant species generally have lower levels of defence against herbivores than do plants with a slow growth rate; positive effects of plant vigour are thus more likely to occur (Herms & Mattson, 1992; Loehle, 1996; Zangerl *et al.*, 1997).

Price *et al.* (1980) stressed that studies on population dynamics of herbivorous insects should, in addition to plant–herbivore interactions, consider three-trophic-level cascading phenomena. The work reported here demonstrates that the size of both moths (Figs 3 and 4) and parasitoids was related positively to plant vigour (Figs 5d–f and 6d–f). As far as population dynamics is concerned, however, the relative extent of this effect on the two trophic levels is what matters. This study showed that the effects of plant vigour on insect size were consistently stronger in moths than in their parasitoids (Figs 5a–c and 6a–c). As such, this difference does not necessarily imply similar biases in reproductive potentials as the effect of body size on fitness may vary among taxa. To derive conclusions about population dynamics, it is also necessary to examine the dependence of expected realised fecundity on body size in the species involved.

In insects, the body size–fitness relationship appears to depend on the presence of adult feeding. The potential fecundity of capital breeders (vs. income breeders; terminology first used by Drent & Daan, 1980), i.e. species with non-feeding adults, is typically correlated strongly with female body size (Istock, 1967; Honěk, 1993; Tammaru & Haukioja, 1996; Taylor *et al.*, 1998). The strength of this relationship is apparently based on two complementary mechanisms. First, in a non-feeding adult, reproductive potential is limited by the resources accumulated during the larval stage (\approx pupal weight). Second, due to relatively simple reproductive behaviour and short lifetime of capital breeders, there tends to be a straightforward link between potential and realised fecundity in those insects (Tammaru & Haukioja, 1996; Tammaru *et al.*, 1996). In contrast, the relationship between body size and realised fecundity in income breeders (i.e. insects in which adult feeding is crucial for reproduction) is often shown to be less clear (e.g. Karlsson & Wiklund, 1984; Braby & Jones, 1995). The fecundity of these insects depends primarily on resources available for adults rather than weight at eclosion. Long adult life and complex reproductive behaviour of income-breeding insects further obscure the physiological link between large size and fecundity in complex environments: realised fecundity may be very different from potential fecundity (Leather, 1988; Tammaru & Haukioja, 1996).

The studied moths, *N. typhae* and *A. sparganii*, do not feed as adults, being thus capital breeders. The number of eggs as the index of potential fecundity is therefore presumably a satisfactory measure of their realised fecundity. On the other hand, the parasitoids in this system represent income-breeding hymenopterans (Hinz, 1983, 1991; T. Teder, pers. obs.). In addition to dependency on resources for adult feeding, several features common to parasitoids' life histories may weaken further the relationship between body size and potential fecundity in these insects compared with their capital-breeding hosts (Hardy *et al.*, 1992; Ellers & van Alphen, 1997). If the period when hosts are vulnerable to parasitoid attacks is short, the relationship between body size and realised fecundity is presumably weakened as parasitoids have to share time

among feeding, searching for hosts, and ovipositing. Moreover, the realised fecundity of parasitoids depends critically on the encounter rates with suitable hosts, the distribution of which may vary both spatially and temporally. A straightforward link between resource level and reproductive success can thus be expected in capital breeders, the situation being quite different in income breeders. Such a difference can have consequences for community and population dynamics: bottom-up regulation is more likely in capital breeders.

Weaker plant quality–body size and body size–fitness relationships suggest that, in terms of fitness, the studied parasitoids gained less from an increase in plant vigour than did the moths. This implies that the numerical response of the herbivore population to a change in plant quality should exceed the response of the parasitoids. Thus, in the short term, a favourable change in the quality of *Typha* should lead to increased population densities of the moths and lower total parasitism rates. This study showed that in *T. latifolia*, substantial and rapid changes in vigour are possible: in 1995 and 1996 there was a more than twofold difference in height of shoots. Direct documentation of the effects of plant quality on the transgenerational dynamics of the insect community would, however, require longer time series.

Tammaru and Haukioja (1996) discussed factors that may explain the relatively frequent occurrence of eruptive dynamics in capital-breeding herbivorous insects compared with income breeders. The work reported here hints at a possible additional explanation for this tendency. If a capital-breeding herbivore is attacked by an income-breeding parasitoid(s), a rapid increase in plant quality may affect herbivore fitness to an extent where its population may escape regulation by parasitoids. This would be the case due to a weaker corresponding numerical response of the parasitoid population to plant quality. The results thus imply that adult feeding in both herbivores and their parasitoids may be an important aspect to consider in the population dynamics of host–parasitoid systems in general. This logic may well be reversed in a system where an income-breeding herbivore is attacked by a capital-breeding parasitoid: a change in plant quality may then have a stronger effect on the reproductive potential of the parasitoid population.

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