

Fertility and the food quality of wetland plants: a test of the resource availability hypothesis

S. J. McCanny, P. A. Keddy, T. J. Arnason, C. L. Gaudet, D. R. J. Moore and B. Shipley

McCanny, S. J., Keddy, P. A., Arnason, T. J., Gaudet, C. L., Moore, D. R. J. and Shipley, B. 1990. Fertility and the food quality of wetland plants: a test of the resource availability hypothesis. – *Oikos* 59: 373–381.

We tested the resource availability hypothesis of antiherbivore defence with emergent wetland plant species. A physiological measure of the food quality of these species was derived using the growth rates of *Ostrinia nubilalis* larvae on agar-based diets with plant secondary compounds and fiber incorporated at 20% of their concentration in fresh leaf tissue. The correlations between food quality and the weighted mean and median positions of these species along four different fertility gradients were examined. No correlations were found. Similarly, there was no correlation between food quality and the maximum relative growth rates of these plants as seedlings. These results and others in the literature point to the lack of generality in the food quality predictions made by optimal defence theory.

S. J. McCanny, Dept of Biology, Univ. of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 0W0. – P. A. Keddy, T. J. Arnason, C. L. Gaudet and D. R. J. Moore, Dept of Biology, Univ. of Ottawa, Ottawa, Ontario, Canada K1N 6N5. – B. Shipley, Dept of Biology, McGill Univ., 1205 Ave. Dr Penfield, Montreal, Quebec, Canada H3A 1B1.

Introduction

Life history theory is largely derived from the observation of negative correlations between character traits which reasonably can be supposed to draw upon the same resource base (Southwood 1988). The traits involved in these “trade-offs” often can be linked to driving variables in the environment (Grime 1979, Southwood 1988). The net result is that broad predictions can be made about the characteristics of organisms living in a given environment.

A recent example of this approach is the prediction that antiherbivore defences in plants should be more effective in habitats with low resource availability (Coley et al. 1985). This prediction is based upon a trade-off between maximum growth rate and defence investment. It has proven difficult to detect a measurable cost of defence investment in terms of lost potential for growth or reproduction (Simms and Rausher 1987, Brown 1988; but see Coley 1986) and therefore difficult to

make a case for a defence model that is based on trade-offs. Nonetheless, the prediction of variation in the level of herbivory along resource gradients is an attractive alternative to the “apparency” hypotheses of Feeny (1976) and Rhoades and Cates (1976), for at least three reasons:

- 1) The resource availability hypothesis for antiherbivore defence has been incorporated into Southwood's (1988) generalized habitat templet model and so could lead to a general model for antipredator defence.

- 2) In addition to the qualitative predictions made by the apparency hypotheses about the type of secondary chemicals used for defence, Coley et al. (1985) make quantitative predictions about the level of herbivory in the vegetation of a given habitat.

- 3) It would appear easier, at least at first glance, to quantify resource availability than apparency, the availability of plants to their herbivores.

Our approach to testing this hypothesis arises out of the tradition of comparative plant ecology (Rorison et

Accepted 20 August 1990

© OIKOS

wise, our measure of food quality would only apply to this single introduced pest species. It certainly cannot be argued that highly polyphagous organisms are specifically adapted to each of the wide variety of defensive chemicals that they encounter in their diet. The assumption of correlation between food value estimates based on different generalist herbivores has held up well in previous studies (Reader and Southwood 1981, Mac Lean and Jensen 1985, Rathcke 1985).

Diet preparation and bioassay

Leaf tissue was homogenized and filtered under suction (Whatman#1). The filtrate was dried to a residue in a roto-evaporator and then taken up again in 5 ml of 95% ethanol. The unextracted fiber was dried at 60°C, scraped off the filter paper and ground in a Wiley mill.

The ethanol extract and fiber components of each plant species were incorporated into diet cubes at 20% of their concentration in fresh leaf tissue. The concentrated extract (4 ml) was added to a tared beaker and then dried to a residue under N₂. The residue was solubilized with 0.5 ml of 95% ethanol. Eighty percent of the dry weight of the powdered fiber taken from the same 10 g tissue sample was also added to the beaker. A hot (35–40°C) corn-agar diet mixture (Guthrie et al. 1972) was added to achieve a total weight of 40 g and the entire mixture was allowed to set in a mold yielding twenty diet cubes (≈ 2 g each). A control diet was prepared with 0.5 ml ethanol and 40 g of the corn-agar diet mixture.

Individual third instar larvae (≈ 2 wk old) were weighed and then placed in cotton plugged vials with single diet cubes. They were incubated in a growth cabinet at 26°C/19°C day-night temperature regime, 90% relative humidity and a 18:6 L:D photoperiod for a total of eight days. Between 15 and 20 larvae were tested for each plant species. For every set of four plant species that were tested, twenty larvae were grown on control diets. At the end of the eight day growth period all the larvae were weighed and their growth rates were calculated as the difference between the natural logarithms of the final and initial weights divided by the growth period. The Food Quality Index (FQI) for each species was calculated as the ratio between the mean larval growth rate for that species and the mean growth rate of the accompanying control larvae.

Field survey

Three study locations were chosen in Eastern Ontario, Canada (Westmeath and Presqu'île) and Western Quebec (Luskville). At each study location, five sites of varying standing crop were selected. The Presqu'île study location (44°0'N, 77°43'W) is a peninsula located on the north Lake Ontario shoreline within Presqu'île

Provincial Park. The sites surveyed included two low standing crop (1–400 g m⁻²) wet meadows, a moderate standing crop (200–500 g m⁻²) fen, a high standing crop (400–900 g m⁻²) marsh and a very high standing crop (800–2500 g m⁻²) *Typha* marsh. The Westmeath study location (45°47'N, 76°50'W) is a riverine shoreline located on the Ottawa River 22 km southwest of the city of Pembroke. At this location, we surveyed two open beach sites with low standing crops as well as a moderate and a high standing crop marsh located in Bellows Bay. A very high standing crop *Typha* marsh located 15 km south of Westmeath was also surveyed. The Luskville study location (45°31'N, 76°6'W) is also a riverine shoreline located 5 km west of Luskville, Quebec on the Ottawa River. The survey included two low standing crop shoreline sites, moderate and high standing crop sheltered marshes, and a very high standing crop *Typha* marsh.

The study locations were surveyed 12–14 September, 1986 (Presqu'île), 19–19 August, 1987 (Luskville) and 25–26 August, 1987 (Westmeath). At each of the five sites representing different levels of standing crop, fifteen quadrats (0.5 m × 0.5 m) were randomly chosen. Each quadrat was divided into nine equivalent subsections. The abundance of each species in a given quadrat was estimated by the number of subsections in which it occurred (0–9). The vegetation in each quadrat was clipped at ground level, dried to constant biomass at 60°C and weighed to determine standing crop. A total of 141 species were identified in the 225 quadrats examined at these three locations.

Soil analysis and a stoichiometric index

As part of the survey, five soil cores (10 cm depth, 3 cm diameter) were taken from each quadrat; one core from the center and one from each corner. These samples were pooled, frozen within eight hours and subsequently analyzed together. Chemical analyses were performed by Agri-Food Laboratories in Guelph, Ontario. Nitrates were extracted in deionized water and assayed with an ion selective electrode (McKeague 1978). Total phosphorus was measured by the sodium bicarbonate extractable method and potassium and magnesium were assayed by the ammonium acetate extraction method (McKeague 1978).

The concentrations of each of these nutrients varies along an independent gradient. We attempted to combine these values into a single index of fertility by comparing the ratios of nutrients found in the soil to the stoichiometric ratios in which they combine in wetland plant tissues. We assumed that all species in our study have identical nutrient concentrations and therefore identical long term requirements. This can be justified in light of the minor variations in nutrient tissue concentrations between wetland species and across sites (Boyd 1978). We further assumed that the various extraction

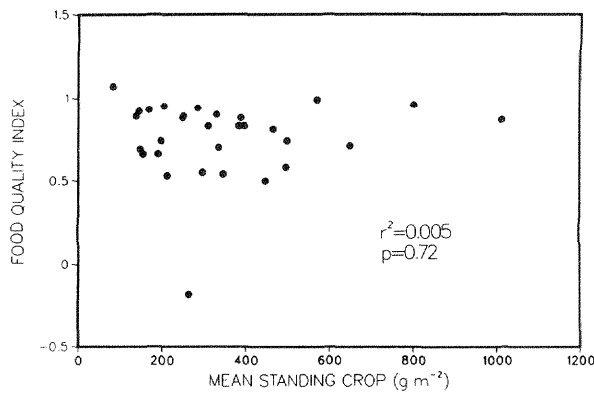


Fig. 2. Scatter diagram of the relationship between the food quality index of a plant species and the weighted mean standing crop of the quadrats in which it occurred.

Results

Appendix 1 lists the food quality indices for the forty two species of wetland plants for which fertility or maximum growth rate data were available. The values ranged from slightly greater than one, indicating enhanced growth rates from the incorporation of plant extract and fiber into *O. nubilalis* diets, to less than zero, indicating weight loss and toxic effects by the species involved. The species that prevented positive growth, *Solidago graminifolia* and *Coreopsis rosea*, were both from the Asteraceae. The only appreciable mortality occurred among the larvae feeding on a *S. graminifolia* diet. Nine of the nineteen larvae in this group did not survive the eight day test period. When these toxic species were excluded, the food quality index of the remaining forty species ranged from 1.07 to 0.50. This group was composed of graminoids and forbs in equal proportions. There was no significant difference in the mean food quality indices of the non-toxic forbs and the graminoids ($t_{\text{obs}} = 0.06$; $df = 38$).

Intraspecific variation in food quality was examined for two common species, *Lythrum salicaria*, a forb, and *Phalaris arundinacea*, a graminoid. Each species was sampled in four different localities and their tissues

were separately incorporated into diet cubes. The effect of these separate samples on the growth rates of *O. nubilalis* larvae is shown in Table 1. The *P. arundinacea* diets consistently suppressed growth more than the *L. salicaria* diets and the variation within species was similar.

Fig. 1 demonstrates the distribution of thirty species along a standing crop gradient. These are the species for which food quality data were available and that occurred in more than five quadrats in the vegetation survey of the Presqu'ile, Westmeath and Lusville locations. Table 2 shows that the mean and median fertility values for these species varied over one to two orders of magnitude. Nonetheless, food quality was unrelated to either the mean or the median position of species on any of the four fertility gradients examined (Fig. 2; Table 2). A comparison of food quality between the species collected in the nutrient-rich Ottawa Valley habitats and those collected in the nutrient-poor Wilson's Lake habitat showed no difference ($t_{\text{obs}} = 0.84$; $df = 40$). Similarly, there was no relationship between food quality and the relative growth rate of thirty two plant species as seedlings (Fig. 3). The lack of correlation in Figs 2 and 3 was not affected by the elimination of the outlying toxic species.

Discussion

Intraspecific variation

In correlating species characteristics, it is important to consider their intraspecific variation. If there is more variation within species than between species then the characteristic is inappropriate for comparisons across species. Table 1 demonstrates that the ranges of food quality in two species are considerably less than that for the entire data set. It is possible, of course, that several species in our study have wide intraspecific variation in food quality. One would then expect a random relationship between the food quality of single collections and the mean positions of these species along a nutrient gradient.

Several species showed considerable variation in their position along a standing crop gradient (Fig. 1). In

Table 2. The range of eight measures of species position on fertility gradients for thirty species of wetland plants and the Pearson correlation coefficient (r) between each measure and the food quality index. All regressions are non-significant at $p = 0.05$.

Fertility measure	Maximum	Minimum	r
Mean standing crop (g m^{-2})	1012.8	83.2	0.07
Median standing crop (g m^{-2})	1739.2	22.8	-0.04
Mean stoichiometric fertility index	9.3	1.9	0.19
Median stoichiometric fertility index	19.9	1.8	-0.05
Mean soil nitrate content (ppm)	21.0	4.3	0.12
Median soil nitrate content (ppm)	86.0	3.0	-0.14
Mean soil phosphorus content (ppm)	19.9	3.3	0.14
Median soil phosphorus content (ppm)	18.0	1.0	-0.02

conditions. The “fertile” species are expected to have an innate tendency to make low allocations of resources to defence and therefore to have high food quality (Coley et al. 1985). This tendency should be enhanced if these species are grown under a fertile growth regime (Chapin, pers. comm.). Our study design should make the discovery of a correlation between food value and position on a fertility gradient more likely than would be the case for an experimental design where the tissues for food value analysis were grown under the same nutrient regime. Nonetheless, we did not find such a correlation.

Our study combines quantitative estimates of resource availability with a physiological estimate of food value. It represents the most detailed and extensive test to date of the relationship between these variables. The lack of correlation between them, even in the extreme case of a lack of difference between the food quality of the Wilson’s Lake flora and the Ottawa Valley flora, suggests that there is little generality to the predicted relationship. Part of the reason for this lack of correlation is the lack of correlation between maximum growth rate and position along a fertility gradient (McCanny, pers. obs.). This goes counter to Grime’s (1979) predictions for growth rate and stress. A further possibility is that structural features of the plants under consideration could act secondarily as a defence against herbivory. The reeds (leafless plants) in our study have fibrous support structures which likely serve a defence function as well. These species may not have been selected for further defences through either herbivore tolerance or avoidance. We did not measure leaf toughness, so this defence capacity would not be included in our estimate of food value. Since reeds occur across a broad range of fertilities, they could introduce considerable scatter to a hypothetical resource-food value relationship. However, removing the reeds from the data set does not improve the relationship in Fig. 2 ($r^2 = 0.01$; $n = 23$).

Support for a relationship between resource availability and food value is essentially restricted to the references in Coley et al. (1985). Upon searching the recent literature, we can only add one reference. Mills (1986) provides anecdotal evidence that the Californian chaparral has less fertile soil and less herbivore damage than the Chilean matorral. The clearest example of such a relationship is Coley’s (1983) seminal work on herbivory in sun-demanding (high resource) and shade-tolerant (low resource) saplings in the light gaps of tropical forests. Newberry and de Foresta (1985) were unable to replicate Coley’s (1983) results, finding no difference in the levels of herbivory in shade-tolerant and sun-demanding saplings grown in full sunlight. Interestingly, they found the lowest levels of phenolics and the highest levels of herbivory among shade-tolerant species growing in the primary forest understory. This result may be explained as the result of light regulation of the synthesis of phenolics (Swaine and Harborne 1979). In a

similar vein, Baldwin and Schultz (1988) found higher levels of phenolics among sun-demanding species of *Miconia* than for shade-tolerant members of the same genus grown in full sunlight. This suggests higher levels of defence investment or lower food quality in species adapted to high resource availability and faster growth rates. Under the assumptions of the mathematical model in Coley et al. (1985), the tendency for plants adapted to low resource environments to defend their tissues as little as or less than plants of high resource environments can only be explained if potential losses to herbivory are consistently lower in the low resource environments under consideration. Measurements of potential herbivore pressure would provide a useful complement to future studies of the resource availability hypothesis.

Conclusions

The picture that is emerging is that optimal defence theory is still unable to make general predictions about the food quality of plants to their herbivores, whether these predictions are based on apparency or resource availability. Both these predictors are multi-faceted and difficult to measure and this contributes to their lack of utility in predicting food quality. Nonetheless, there appears to be much potential in such variables as the life expectancy (Southwood et al. 1986) and regrowth capability (van der Meijden et al. 1988) of leaves in determining their suitability as food for herbivores.

Acknowledgements – We thank T. Chapin, and M. J. Lechowicz for constructive criticism of this manuscript. Much thanks to J. Belcher, N. Donskov and C. McJanet for technical assistance. I. Wisheu collected leaf tissue in Nova Scotia. This research was made possible through grants from the Canadian Shield Foundation (P.A.K.), the Univ. of Ottawa (P.A.K.), the Ontario Ministry of Agriculture and Food (T.J.A.) and NSERC (P.A.K. & T.J.A.).

References

- Arnason, J. T., Borque, G. J., Madosingh, C. and Orr, W. 1986. Disruption of membrane functions in *Fusarium culmorum* by an acetylenic allelochemical. – *Biochem. Syst. Ecol.* 14: 569–574.
- , Philogène, B. J. R., Donskov, N. and Kubo, I. 1987. Liminoids from the Meliaceae and Rutaceae reduce feeding, growth and development of *Ostrinia nubilalis*. – *Ent. exp. appl.* 43: 221–226.
- Baldwin, I. T. and Schultz, J. C. 1988. Phylogeny and the patterns of leaf phenolics in gap and forest adapted *Piper* and *Miconia* understory shrubs. – *Oecologia (Berl.)* 75: 105–109.
- Boyd, C. E. 1978. Chemical composition of wetland plants. – In: Good, R. E., Whigham, D. F. and Simpson, R. L. (eds), *Freshwater wetlands: Ecological processes and management potential*. – Academic Press, New York, pp. 155–167.

Appendix 1. Food quality index and relative growth rate (d^{-1}) of plant species fed to *Ostrinia nubilalis* larvae. Taxonomy follows Gleason and Cronquist (1963).

Species	Food Quality Index	Relative growth rate	Growth form	Collection site
<i>Artemisia campestris</i>	1.07	0.21	F	OT
<i>Polygonum coccineum</i>	1.03	0.27	F	OT
<i>Sagittaria latifolia</i>	0.99	–	G	OT
<i>Rumex verticillatus</i>	0.96	0.20	F	OT
<i>Verbena hastata</i>	0.96	0.26	F	K
<i>Gnaphalium uliginosum</i>	0.95	0.29	F	OT
<i>Iris versicolor</i>	0.94	0.14	G	OT
<i>Juncus effusus</i>	0.93	0.18	GR	OT
<i>Juncus bufonius</i>	0.92	0.19	G	OT
<i>Eleocharis palustris</i>	0.90	0.10	GR	OT
<i>Eriocaulon septangulare</i>	0.89	0.01	GR	WL
<i>Eleocharis ovata</i>	0.89	0.24	GR	OT
<i>Eupatorium perfoliatum</i>	0.88	0.25	F	OT
<i>Sparganium eurycarpum</i>	0.88	0.21	G	OT
<i>Typha angustifolia</i>	0.87	0.21	G	MI
<i>Alisma Plantago-aquatica</i>	0.86	–	G	OT
<i>Juncus filiformis</i>	0.86	0.18	GR	OT
<i>Solidago galetorum</i>	0.84	–	F	WL
<i>Bidens cernua</i>	0.83	0.26	F	OT
<i>Triadenum Fraseri</i>	0.83	0.21	F	OT
<i>Scirpus fluviatilis</i>	0.83	–	G	MI
<i>Epilobium ciliatum</i>	0.81	–	F	MI
<i>Lythrum Salicaria</i>	0.81	0.26	F	OT, MI
<i>Sabatia Kennedyana</i>	0.80	0.16	F	WL
<i>Gratiola aurea</i>	0.80	–	F	WL
<i>Carex crinita</i>	0.77	0.19	G	OT
<i>Eleocharis erythropoda</i>	0.74	0.21	GR	OT
<i>Lysimachia terrestris</i>	0.74	–	F	OT
<i>Scirpus acutus</i>	0.71	0.13	GR	OT
<i>Bidens frondosa</i>	0.70	–	F	OT
<i>Spartina pectinata</i>	0.69	0.22	G	OT
<i>Penthorum sedoides</i>	0.66	0.30	F	OT
<i>Mimulus ringens</i>	0.66	0.26	F	OT
<i>Scutellaria lateriflora</i>	0.64	0.23	F	OT
<i>Lycopus uniflorus</i>	0.61	–	F	OT
<i>Phalaris arundinacea</i>	0.58	–	G	OT, MI
<i>Hypericum ellipticum</i>	0.55	0.35	F	OT
<i>Leersia oryzoides</i>	0.54	0.28	G	OT
<i>Scirpus americanus</i>	0.53	0.13	GR	OT
<i>Scirpus cyperinus</i>	0.50	0.19	GR	OT
<i>Coreopsis rosea</i>	–0.01	0.26	F	WL
<i>Solidago graminifolia</i>	–0.18	0.26	F	OT

F = forb, G = graminoid, GR = graminoid reed, OT = Ottawa River, MI = Mississippi River drainage (tributary of Ottawa R.), K = Wildflower garden in Ottawa, WL = Wilson's Lake, Nova Scotia.

- Brown, D. G. 1988. The cost of plant defense: an experimental analysis with inducible proteinase inhibitors in tomato. – *Oecologia* (Berl.) 76: 467–470.
- Bryant, J. P. and Kuropat, P. J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. – *Ann. Rev. Ecol. Syst.* 11: 261–286.
- Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. – *Ecol. Monogr.* 53: 209–233.
- 1986. Costs and benefits of defense by tannins in a neotropical tree. – *Oecologia* (Berl.) 70: 238–241.
- 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. – *Oecologia* (Berl.) 74: 531–536.
- , Bryant, J. P. and Chapin, F. S. III 1985. Resource availability and plant antiherbivore defense. – *Science* 230: 895–899.
- Day, R. T., Keddy, P. A., McNeill, J. and Caleton, T. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. – *Ecology* 69: 1044–1054.
- Feeny, P. P. 1976. Plant apparency and chemical defense. – In: Wallace, J. and Mansell, R. L. (eds), *Biochemical interactions between plants and insects*. *Rec. Adv. Phytochem.*, vol. 10. Plenum Press, New York, pp. 1–40.
- Gleason, H. A. and Cronquist, A. 1963. *Manual of vascular plants of northeastern United States and adjacent Canada*. – D. Van Nostrand, Princeton, NJ.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. – Wiley, Chichester, England.
- and Hunt, R. 1975. Relative growth-rate: its range and adaptive significance in a local flora. – *J. Ecol.* 63: 393–422.
- Guthrie, W. D., Russel, W. A. and Jennings, C. W. 1972. Resistance of maize to second brood European corn borer. – *Proc. 26th Ann. Corn-Sorghum Conf.*: 165–179.
- Hudon, M. and Le Roux, E. J. 1986. Biology and population dynamics of the European corn borer (*Ostrinia nubilalis*) with special reference to sweet corn in Quebec. I. Systematics, morphology, geographical distribution, host range, economic importance. – *Phytoprotection* 67: 39–54.
- Hutchinson, G. E. 1975. *Limnological botany*, vol. 3. – A treatise on limnology. Wiley, New York.
- Kaffrey, D. J. and Worthy, L. H. 1927. A progress report on the investigation of the European Corn Borer. – U.S.D.A. Dept. Bull. # 1476.
- Keddy, P. A. 1984. Plant zonation on lakeshores in Nova Scotia: A test of the resource specialization hypothesis. – *J. Ecol.* 72: 792–808.
- 1985. Lakeshores in the Tusket River valley, Nova Scotia: Distribution and status of some rare species, including *Coreopsis rosea* Nutt. and *Sabatia kennedyana* Fern. – *Rhodora* 87: 309–320.
- 1989a. Competition. – Chapman and Hall, London.
- 1989b. Comparative hierarchies and centrifugal organization in plant communities. – In: Grace, J. and Tilman, D. (eds), *Perspectives on plant competition*. – Academic Press, New York.
- MacLean, S. F., Jr. and Jensen, T. S. 1985. Food plant selection by insect herbivores in Alaskan arctic tundra: the role of plant life form. – *Oikos* 44: 211–221.
- McKeague, J. AS. (ed.) 1978. *Manual on soil sampling and methods of analysis*. – Canadian Soc. Soil Sci., Ottawa, Ontario, Canada.
- McKey, D., Waterman, P. G., Mbi, C. N., Gartlan, J. S. and Struhsaker, T. T. 1978. Phenolic content of vegetation in two African rain forests: ecological implications. – *Science* 202: 61–64.
- Meijden, E. van der, Wijn, M. and Verkaar, H. J. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. – *Oikos* 51: 355–363.
- Mills, J. N. 1986. Herbivores and early postfire succession in southern California chaparral. – *Ecology* 67: 1637–1649.
- Newberry, D. McC. and de Foresta, H. 1985. Herbivory and defense in pioneer, gap and understory trees of tropical rain forest in French Guiana. – *Biotropica* 17: 238–244.
- Oram, R. N. and Williams, J. D. 1967. Variation in concentration and composition of toxic alkaloids among strains of *Phalaris tuberosa* L. – *Nature*, Lond. 213: 946–947.
- Rathcke, B. 1985. Slugs as generalist herbivores: test of three hypotheses on plant choice. – *Ecology* 66: 828–836.
- Reader, P. M. and Southwood, T. R. E. 1981. The relationship between palatability to invertebrates and the successional status of a plant. – *Oecologia* (Berl.) 51: 271–275.
- Rhoades, D. F. and Cates, R. G. 1976. Towards a general theory of plant antiherbivore chemistry. – *Rec. Adv. Phytochem.* 10: 168–213.
- Rorison, I. H., Grime, J. P., Hunt, R., Hendry, G. A. F. and Lewis, D. H. 1987. Frontiers of comparative plant ecology. – *New Phytol.* 106 (suppl): 1–317.
- Sheldon, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. – *Ecology* 68: 1920–1931.
- Shipley, B. and Peters, R. H. (in press). Test of the Tilman model of plant strategies: relative growth rate and biomass partitioning. – *Am. Nat.*
- Simms, E. L. and Rausher, M. D. 1987. Costs and benefits of plant resistance to herbivory. – *Am. Nat.* 130: 570–581.
- Southwood, T. R. E. 1988. Tactics, strategies and templates. – *Oikos* 52: 3–18.
- , Brown, V. K. and Reader, P. M. 1986. Leaf palatability, life expectancy and herbivore damage. – *Oecologia* (Berl.) 70: 544–548.
- Swaine, T. and Harborne, J. B. 1979. *Biochemistry of plant phenolics*. – Plenum Press, New York.
- Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press, Princeton, NJ.
- Warther, J. D., Redfern, R. E., Uebel, E. C. and Mills, G. D. 1982. Antifeedant screening of 39 local plants with fall armyworm larvae. – *J. Environ. Sci. Health A17*: 885–895.
- Wisheu, I. C. and Keddy, P. A. 1989. The conservation and management of a threatened coastal plain plant community in eastern North America (Nova Scotia, Canada). – *Biol. Cons.* 48: 229–238.

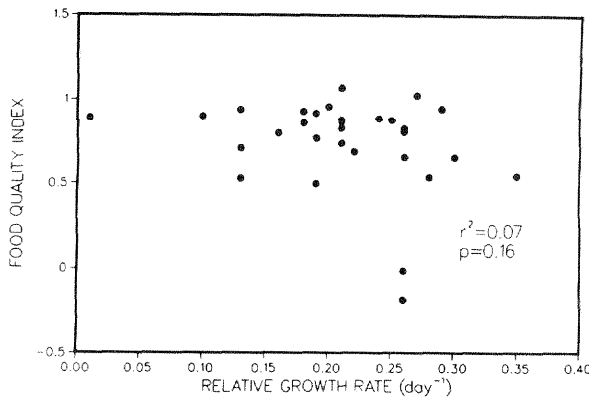


Fig. 3. Scatter diagram of the relationship between the food quality index of a plant species and its relative growth rate as a seedling.

particular, three species occurred at very low standing crops ($< 8 \text{ g m}^{-2}$) as well as at moderately high standing crops ($\approx 600 \text{ g m}^{-2}$). This seems to indicate an ability to withstand high levels of disturbance rather than low levels of nutrients (Day et al. 1988). Most species were found in the $100\text{--}400 \text{ g m}^{-2}$ range of standing crop and few species had mutually exclusive ranges. Nonetheless, the distributions tended to be unimodal and leptokurtic (i.e. exhibiting a high maximum frequency; not shown in Fig. 1). As a result, species with similar standing crop ranges tended to have different weighted mean and median standing crop values.

Species with low food quality

Unlike MacLean and Jensen (1985), we did not find that forbs had consistently higher food quality than graminoids. Of course, we did not present intact plant tissues to the *O. nubilalis* larvae and so the physical differences between plants were minimized.

There were few surprises among the species with the lowest food quality (Appendix 1). Members of the Asteraceae are known to contain phototoxins, although these are usually most concentrated in inflorescences (Arnason et al. 1986). It should be noted that other members of the Asteraceae (esp. *Gnaphalium uliginosum* and *Artemisia campestris*) were shown to have high food quality. It is surprising that the species that demonstrated the most toxic effects, *Solidago graminifolia*, should be listed by Hudon and LeRoux (1986) as a host species for *Ostrinia nubilalis* in the wild. Perhaps the leaf tissue of this plant differs markedly in food quality from its stem tissue, where *O. nubilalis* is found in nature. The phototoxin hypericine is found in species of the genus *Hypericum*, such as *H. ellipticum* in this study. Another species we found to have low food quality was *Phalaris arundinacea*. This genus has long been noted for its antiherbivore effects (Oram and Williams

1967). *Leersia oryzoides* or cut grass is known for its small, stiff spinules along the edge of leaf blades. This physical defence could well have been preserved in the ground fiber of our artificial diet, conferring a low food quality on this species. The remaining two species with food quality indices less than 0.6 were *Scirpus americanus* and *S. cyperinus*. These reeds would be expected to present physical barriers to chewing insects, however much of this effect would be lost by grinding the plant fiber. Two other members of this genus, *S. fluviatilis* and *S. acutus*, demonstrated intermediate food quality in this study.

Antiherbivore defence theory

The theory detailed in Coley et al. (1985) essentially offers two alternative models for antiherbivore defence in plants: tolerance and avoidance. Species with high growth rates tolerate herbivory and those with low food quality avoid it. Assuming a trade-off between these two "strategies" and assuming that plants with high growth rates dominate habitats with high resource availability, they predicted that both maximum growth rate and resource availability will be positively correlated with food quality. We will consider these predictions individually.

Maximum growth rate and food quality

Although much work supportive of Coley et al. (1985) has been published on the relationships between food quality and life form or successional status (Reader and Southwood 1981, MacLean and Jensen 1985, Rathcke 1985), only four studies have directly tested the relationship between plant growth rate and food quality. Sheldon (1987) and Coley (1988) have demonstrated that rapidly growing plant species are the preferred foods of generalist herbivores. The results of our study and those of van der Meijden et al. (1988) show no such relationship. Van der Meijden et al. (1988), studying dune biennials, did find a positive correlation between herbivore damage and the capacity for regrowth after herbivory. They found this latter variable to be a more cogent descriptor of herbivore tolerance than the growth rate of a plant in the absence of herbivores. Perhaps regrowth rates will provide better predictions of food value than maximum growth rates can.

Resource availability and food quality

We sampled the leaf tissues of the various species in this study without reference to position on fertility gradients. As a result, we tended to sample species that were adapted to high fertility in fertile growing conditions and species adapted to low fertility in infertile

Table 1. Intraspecific variation in the food quality index of two wetland plant species.

	<i>Lythrum salicaria</i>	<i>Phalaris arundinacea</i>
	0.71	0.58
	0.87	0.61
	0.85	0.48
	0.77	0.63
Mean	0.81	0.58
S.D.	0.07	0.07

procedures detect equivalent proportions of the potentially available pool of each nutrient. Finally, we assumed that the nutrient ratios within quadrats and the relative nutrient status between quadrats remain roughly constant throughout the growing season.

The concentration of each nutrient (N, P, K and Mg) in the soil of each quadrat ($\mu\text{g g}^{-1}$ of soil) was divided by its average concentration in wetland plant tissue ($\mu\text{g g}^{-1}$ of plant tissue; Boyd 1978). The resultant ratios have units of grams of plant tissue per gram of soil and represent the maximum efficiency with which soil can be converted to plant tissue if the nutrient under consideration is limiting. The lowest such ratio for a given quadrat would be that of the most limiting nutrient of the four nutrients considered and should be proportional to its fertility. This ratio was taken as the stoichiometric fertility index.

Species positions along fertility gradients

Species abundance values were used to weight fertility indices and calculate the mean and median positions of species along the corresponding fertility gradient. Only species present in more than five quadrats were examined. The four measures of fertility used were standing crop (g m^{-2}), soil nitrate content (ppm), soil phosphorus content (ppm) and the stoichiometric fertility index. The mean fertility for each species (f_i) was calculated as follows:

$$f_i = \frac{\sum a_{ij} b_j}{\sum a_{ij}}$$

where a_{ij} represents the abundance of the i th species in the j th quadrat and b_j represents the fertility of the j th quadrat. The median fertility for each species was calculated by assigning the average fertility of the j th quadrat (b_j) to every subsection of the quadrat containing a given species. The fertilities of these subsection were ranked and the median value was taken as the median fertility for the species.

Maximum growth rates

Plants were grown from seed in commercial potting soil (Fafard Black Earth) in twelve replicate pots (10.5 cm diameter, 9 cm depth) at the McGill University Phytotron. The pots were fertilized with Plant Products water soluble fertilizer. This fertilizer consisted of a 20:20:20 ratio of total nitrogen, available phosphoric acid (P_2O_5), soluble potash (K_2O) plus Fe, Mn, Zn, Cu, B, Mo and a 1% chelated metal complex of EDTA. Six seedlings from each species were harvested ten days after germination and the remainder were harvested at thirty days. Relative growth rate for each species was estimated as the slope of the least squares regression of the natural logarithm of seedling dry weight on time. Due to incomplete germination, the final number of replicates per species was sometimes less than twelve. Subsequent trials under various fertilizer regimes demonstrated that the growth regime was close to optimal (Shipley and Peters in press).

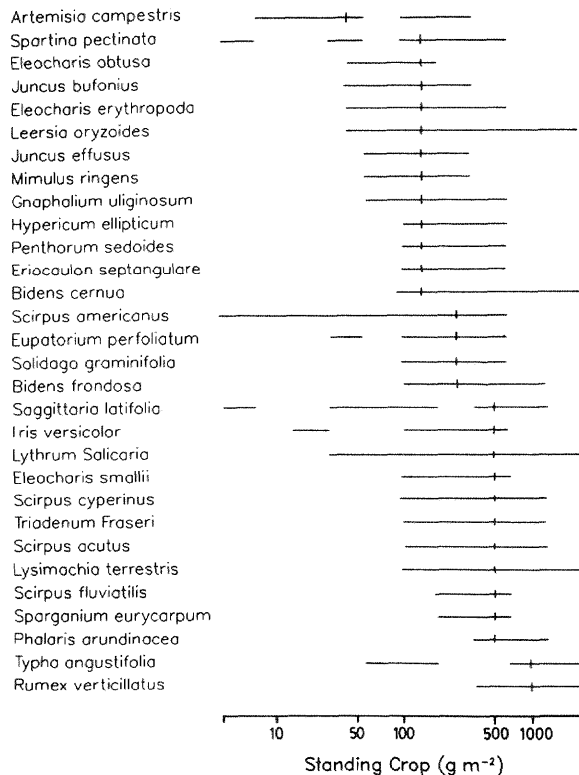


Fig. 1. Distribution of thirty wetland species along a standing crop gradient. Horizontal lines indicate the presence of a species in a logarithmic standing crop interval. Vertical bars indicate the standing crop interval in which a species occurred in the greatest number of quadrat sections.

al. 1987, Keddy 1989a). We set out to screen as many plant species as possible for the traits that theory predicts to be correlated: maximum growth rate, antiherbivore defence capacity and distribution along specific resource gradients. We chose our methodologies accordingly.

The measurement of relative growth rate is a standard procedure in comparative plant ecology (Grime and Hunt 1975). By contrast, there exists a wide range of techniques for assaying defence capacity and a number of possible approaches to examining resource gradients.

We chose a bioassay approach for the measurement of defence. It is well suited to screening a large number of species with diverse morphologies (Reader and Southwood 1981, MacLean and Jensen 1985, Rathcke 1985). Bioassays of defence capacity are usually based on the amount of tissue that a test herbivore will consume under experimental conditions. It is a behavioral measure of food quality. One variation of the bioassay approach involves the comparison of herbivore growth rates on prepared diets incorporating different plant tissues or chemicals (Arnason et al. 1987). This technique focuses on the ability of a generalist herbivore species to metabolize a given plant tissue or phytochemical. It provides a physiological measure of food quality. Although no prepared diet can reconstruct fresh leaf tissue, this approach allows for considerable flexibility when sampling species that are neither abundant nor easily accessible in the field (Warther et al. 1982).

The measurement of resource availability and the position of species along resource gradients also require careful consideration. Resource availability is such a multifaceted concept that variation is usually confined to one or several closely related aspects of the consumable niche requirements (see Tilman 1982) of the species in any given study. Communities of emergent wetland plants are interesting in this respect. The productivity of a wetland stand is not limited by either moisture or sunlight availability. Soil fertility is the predominant aspect of resource availability in these communities (Day et al. 1988). We chose to measure fertility in a number of ways, including estimates of the soil concentrations of single macronutrients (e.g. N and P) and composite indices such as standing crop and a combination of soil characteristics which gives due consideration to the ratios of nutrients required by the vegetation.

Studies of the resource availability hypothesis have tended to contrast the defence capacities of the plant species growing in two different resource states (McKey et al. 1978, Bryant and Kuropat 1980, Coley 1983, Newberry and de Foresta 1985, Baldwin and Schultz 1988). However, in most natural communities, we can expect resource availability to vary along natural gradients (Grime 1979, Tilman 1982, Keddy 1989b). This is especially true in wetland vegetation (Hutchinson 1975, Day et al. 1988). We tested the resource availability hypothesis in wetland habitats by looking for positive cor-

relations among maximum growth rate, food quality and position along fertility gradients.

Methods

Tissue collection

For each plant species, ten grams (fresh weight) of leaf tissue were collected in the field and preserved in 95% ethanol (Warther et al. 1982). The sampling took place in wetland sites along the Ottawa River and the adjoining Canadian Shield lakes, wherever each species could be found in abundance and without reference to their position along fertility gradients. This involved the assumption that the defence characteristics of each species did not vary greatly under different growing conditions. Multiple collections of *Lythrum salicaria* and *Phalaris arundinacea* were made to examine this assumption. Most collections were made at two sites: Luskville and Westmeath (see below). Five species (see Appendix 1) were collected in the infertile wetlands at Wilson's Lake in the Tusket River valley of Nova Scotia, Canada (Keddy 1984, 1985, Wisheu and Keddy 1989). Collections were made late in the growing season (15 Sep–8 Oct) but care was taken to avoid the collection of senescent material. All above ground tissue, including stems and inflorescences, was collected for *Gratiola aurea* and *Gnaphalium uliginosum* because it was too difficult to separate their small leaves from the other tissues. Nine species were leafless reeds (see Appendix 1) and were collected without distinguishing between stem and leaf tissue. Where there was differentiation into flowering and vegetative stalks, only the latter were collected. Petioles and leaf sheaths were excluded. For the smaller species, leaf tissue from many individuals was pooled to make up a 10 g sample. Taxonomy follows Gleason and Cronquist (1963).

Test herbivore

Ostrinia nubilalis (European corn borer) was selected as the test species for the bioassay work. A fully grown, fifth instar larva of this pyralid moth is about 25 mm long and 3 mm wide. *O. nubilalis* is highly polyphagous. It has been shown to attack plants from all the major plant families (Kaffrey and Worthy 1927). Its host range in nature is known to include over 100 species (Hudon and Le Roux 1986). Among its known hosts in Canada are some wetland species, including three of the test species: *Solidago graminifolia*, *Bidens cernua* and *B. frondosa* (Hudon and Le Roux 1986). The larvae were cultured in the laboratory on a corn (maize) based agar diet (Guthrie et al. 1972).

In using only one species of herbivore for our bioassay, we assume that generalist herbivores respond to diverse food sources in broadly similar ways. Other-