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Optimal distribution of defences: are plants smart investors?

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Summary

1. Young leaves often contain higher concentrations of chemical defences than mature leaves. They may be better protected against herbivores because they are more valuable.
2. The youngest leaves of the rosette plants of *Cynoglossum officinale*, contain 50–190 times higher concentrations of pyrrolizidine alkaloid (PA) than old leaves. PAs act as defences against generalist herbivores.
3. We examined a model, which predicts optimal defence allocation in plants, based on the assumptions that photosynthetic activity declines with leaf age, herbivory decreases with increasing PA concentration and PA production is costly but can be reallocated without costs. For optimally distributing plants we predict how the concentration of defences decreases with leaf age.
4. The concentration of defences decreases with increasing resource availability and effectiveness of the defence. Reallocation of defences is most advantageous in slow-growing plants. The distribution of PAs over leaves of *C. officinale* observed in the field can be explained with the model, suggesting that plants indeed are ‘smart’ investors.

Key-words: *Cynoglossum officinale*, defence allocation, herbivory, optimal defence theory, pyrrolizidine alkaloids

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Introduction

Most theories of optimal defence against herbivores compare whole plants that belong to different plant species (Feeny 1976; Coley, Bryant & Chapin 1985; Simms 1992; Yamamura & Tsuji 1995). However, as Janzen (1979) noted, herbivores do not eat ‘Latin binomials’ but usually consume specific plant parts. This is particularly true for small herbivores, such as phytophagous insects. Therefore, the distribution of defences should be considered at the smaller scale that is relevant for insect herbivores (Zangerl & Bazzaz 1992).

The question of how much a plant should invest in defences thus should be accompanied by the question how to distribute these defences over various plant parts. It makes sense that the plant should concentrate its defences in the most valuable parts (McKey 1974; Zangerl & Bazzaz 1992). The value of a plant part can be assessed by removing it and observing the effect of its absence on fitness (Krishik & Denno 1983). Such experiments, especially the removal of young leaves, rather than old leaves depressed the yield of agricultural crops like potatoes and sunflowers (Sackston

1959; Cranshaw & Radcliffe 1980). This is because the photosynthetic capacity of leaves declines with age (Bazzaz 1984; Gulmon & Mooney 1986; Harper 1989).

Cynoglossum officinale L. rosette plants are very suited to test these ideas. The youngest leaf of the rosette has 50–190 times higher levels of pyrrolizidine alkaloids (PAs) than the oldest (van Dam, Verpoorte & van der Meijden 1994). Owing to their high PA-levels, the young leaves are avoided by generalist herbivores (van Dam *et al.* 1995b). Moreover, a damage experiment showed that the removal of the youngest three leaves had a greater negative impact on rosette growth than removal of the oldest three leaves (van Dam 1996).

In this paper we predict the optimal defence distribution that maximizes plant growth, using data from *C. officinale*. We apply a model examined by Iwasa *et al.* (1995), which predicts both optimal amount of PA and optimal distribution over the leaves.

OUTLINE OF THE MODEL

In the model the leaves of a rosette plant are considered as a population of ‘individuals’ of different age,

all contributing to plant growth. Plant growth is maximized if the net production of each leaf over its lifetime is maximized. Chemical defences in the leaves increase the survival of the leaves in presence of herbivores (van Dam *et al.* 1995a).

The problem of how to distribute defences over the leaves is mathematically analogous to the optimal life-history pattern of age-structured populations (Charlesworth 1980). This idea was elaborated by Iwasa *et al.* (1996) who examined a model which calculates the particular age-dependent distribution and amount of chemical defence that attains the maximum relative growth rate, r , i.e. the number of leaves produced relative to the number of leaves present. In the model r is determined implicitly as a real solution of

$$a + bA(0) = \int_0^{x_{\max}} e^{-rx} (f(x) - b \frac{dA}{dx}) e^{-\int_0^x h(A(x')) dx'} dx \quad \text{eqn 1}$$

in which a is the cost of producing a leaf without defence, b the costs of producing one unit of defence chemical, $A(x)$ the age-dependent concentration of the defence chemical, x and x' leaf age, x_{\max} maximum leaf age, $f(x)$ the function for age-specific photosynthetic activity and $h(A)$ herbivory as a function of defence concentration.

Equation 1 shows a clear analogy with the Euler-Lotka equation (Stearns 1992, p. 25). The function to be integrated on the right-hand side of equation is the product of three factors. The first factor, e^{-rx} , indicates that we deal with an exponentially growing leaf population. The second factor, $[f(x) - b dA/dx]$, indicates the amount of energy obtained from a leaf of age x per unit time that can be used to produce new leaves. The third factor quantifies the probability that a leaf will survive to a certain age as a function of its defences. In fact $[f(x) - b dA/dx]$ divided by the cost of producing a new leaf with defences $[a + bA(0)]$, is equal to fertility or the rate of producing new leaves from energy produced by a leaf of age x (Iwasa *et al.* 1996). For any age-dependent allocation schedule $A(x)$, we can easily calculate the relative growth of the plants, using the parameters given in the next section. The mathematics of finding optimal $A(x)$, which results in the highest r , are outlined in Iwasa *et al.* (1996).

The design of the model is based on the following assumptions:

(1) the plants are growing exponentially and constantly produce new leaves, using photosynthetic products; (2) the photosynthetic value of a leaf decreases with leaf age; (3) the fraction of each leaf lost to herbivory decreases with increasing concentration of the defence chemical; (4) the production of defence chemicals entails costs, but their reallocation occurs without costs.

In this paper we only consider exponentially growing plants in a constant environment, which are constantly producing new leaves (Iwasa *et al.* 1996). This also implies that the growth of the plants is limited by

their photosynthesis. In other words, the plants are not nutrient limited but carbon limited.

The photosynthetic activity of leaves of herbs typically declines with leaf age (Mooney & Gulmon 1982; Bazzaz 1984; Harper 1989). Young leaves thus have a greater present and, especially, a greater expected future photosynthetic value than old leaves. For a leaf of age x , its future photosynthetic production is represented by:

$$\int_x^{x_{\max}} f(x') dx' \quad \text{eqn 2}$$

PAs in *C. officinale* deter feeding by generalist herbivores in a dose-dependent way: old leaves with low PA levels are more acceptable than young leaves with high PA levels (van Dam *et al.* 1995b). Iwasa *et al.* (1996) examined two non-linear functions which may fit the dose-response curve:

$$h(A) = h_0 e^{-cA} \quad [\text{exponential}] \quad \text{eqn 3}$$

$$h(A) = \frac{h_0}{(1 + cA)^k} \quad [\text{hyperbolic}] \quad \text{eqn 4}$$

where $h(A)$ is herbivory as a function of the PA concentration, A , h_0 is the rate of herbivory in leaves without PAs, indicating the herbivore pressure in the habitat, and both c and k indicate the effectiveness of PAs as deterrents. Both equations are decreasing functions, but their tails differ quantitatively, which influences the shape of the $A(x)$ curve (Iwasa *et al.* 1996).

Finally, the model assumes, like many other optimal defence models (Coley *et al.* 1985; Gulmon & Mooney 1986; Simms 1992; Zangerl & Bazzaz 1992) that both PA production and leaf construction are costly. PAs in *C. officinale* rosettes can be reallocated without losses (van Dam *et al.* 1995a) and we assume without costs. Firstly, the model will be evaluated for plants that do reallocate their defences. Additionally, we will calculate the selective value of reallocation of defences by comparing r^* of allocation and non-allocating plants.

All parameters are, if applicable, expressed in units of fresh weight, because herbivores consume in units of fresh weight and experience PA concentrations as present in fresh leaf material.

Materials and methods

PLANT SPECIES

Cynoglossum officinale is a facultative biennial that is commonly found on the calcareous coastal sand dunes in the Netherlands and throughout the temperate zones of Europe and Asia (de Jong, Klinkhamer & Boorman 1990). After germination, the seedlings form a tap-root and a rosette. The leaves die back in autumn. Flower primordia are formed during winter provided that rosettes had attained the minimum required size for vernalization (de Jong, Klinkhamer & Prins 1986). The plants contain several types of

pyrrolizidine alkaloids, which serve as anti-feedants against generalist insect herbivores (van Dam *et al.* 1995b).

NET PRODUCTION

The photosynthetic capacity of single leaves was measured on three intact, growth-room grown, rosette plants of *C. officinale* with eight leaves each. The rate of CO₂ exchange, corrected for dark respiration, was measured with a differential gas-analysis system under optimal conditions for light, CO₂ concentration, temperature and humidity (Larcher 1975). The saturating light level for *C. officinale* leaves was determined on the youngest, fully expanded leaf as 729 μmol m⁻² s⁻¹. The air in the closed chamber contained 360 ppm CO₂, at T = 25 °C and relative humidity 80%. After the measurements, the leaf area of every single leaf was measured. The photosynthetic activity per unit leaf area (in μmol CO₂ m⁻² s⁻¹) thus could be converted into the photosynthetic activity per leaf (μmol CO₂ s⁻¹). Assuming a photoperiod of 12 h, a construction cost per g dry weight of 2.69 g CO₂ (Gulmon & Mooney 1986) and a DW/FW ratio of 0.20, the gross photosynthetic production, expressed as the contribution of each leaf to plant growth (gFW day⁻¹) was calculated. In general, only 30% of the carbon budget of slow-growing species like *C. officinale* is invested in leaf growth (Poorter, Remkes & Lambers 1990). Therefore, we multiplied the gross photosynthetic production by 0.3 to obtain the photosynthetic production that attributes to leaf growth, to which we refer as 'net production' (Fig. 1). The youngest leaf of the rosettes was too small to measure photosynthetic activity. Because these leaves are still folded and thus probably are hardly photosyntheti-

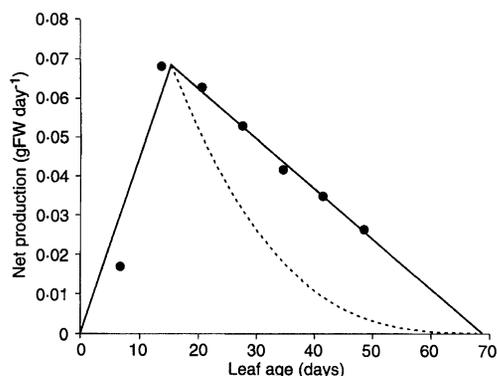


Fig. 1. Net production of leaves of *Cynoglossum officinale*, expressed as the contribution of a leaf of age x to plant growth (g FW per day; photoperiod = 12 h). Data were corrected for respiration and allocation to roots. Filled squares: measured data points. Solid line: linear regression on data points: for $0 \leq x < 15.7$: $y = 0.0044x$, $R_2 = 0.90$ and for $15.7 \leq x \leq 69$: $y = -0.0013x + 0.0889$, $R_2 = 0.99$. Dashed line: alternative $f(x)$ curve in which shading of older leaves was taken into account. For $15.4 \leq x \leq 69$: $y = f_{\max}[(x_{\max} - x)/(x_{\max} - x_1)]^3$.

cally active, their value was set to zero (see also Bazzaz 1984; Harper 1989). The relation between the net production (data points in Fig. 1) and leaf age was analysed with linear regression analysis (see legend to Fig. 1).

The net production of *C. officinale* leaves reaches a maximum of 0.0685 gFW day⁻¹ in leaves which have an age of 15.7 days (intersection of the two regression lines, Fig. 1), after which it gradually declines to zero. This picture is similar to that of other herbaceous plants species (Larcher 1975; Chabot & Hicks 1982; Mooney & Gulmon 1982; Bazzaz 1984; Harper 1989). By extrapolation of the second regression line, we found that the estimated end of photosynthetic activity of a leaf occurs at 69 days after emergence. The maximal leaf age was also measured between August and November 1993 on 30 rosettes growing in sand dunes, the natural habitat of *C. officinale*. On average, leaves stayed completely green for 60 days and they were brown and dead at 82 days after emergence. Our earlier predictions that photosynthetic activity reaches zero at 69 days after emergence, nicely fits these data. The maximum age of a leaf, x_{\max} , was thus set to 69 days. Because leaf life spans tend to decline at the end of the growing season (Bazzaz 1984; Jurik & Chabot 1986), our estimate should be considered as a minimum value.

The age-dependent net production of leaves of *C. officinale* thus is described by the following set of equations:

$$f(x) = \left(\frac{f_{\max}}{x_1} \right) \quad \text{for } 0 \leq x < x_1 \quad \text{eqn 5a}$$

$$f(x) = \frac{f_{\max}}{(x_{\max} - x_1)} (x_{\max} - x) \quad \text{for } x_1 \leq x < x_{\max} \quad \text{eqn 5b}$$

$$f(x) = 0 \quad \text{for } x \geq x_{\max} \quad \text{eqn 5c}$$

in which x_1 denotes the age at which maximum net production, f_{\max} , is attained. In the case of *C. officinale* $x_1 = 15.7$ days, $f_{\max} = 0.0685$ and $x_{\max} = 69$ days (Fig. 1).

By integration of the surface under the functions in Fig. 1, the future contribution of a leaf to growth can be expressed as a function of its age (Fig. 2). From Fig. 2 we derived that within 23 days a leaf has contributed 1 g FW to plant growth (dashed line), which pays back the investments necessary to construct it.

HERBIVORY AS A FUNCTION OF PA CONCENTRATION

The relative herbivory as a function of PA concentration was determined with 2nd and 3rd stage *Spodoptera exigua* Hübner. These larvae are very polyphagous and known to be sensitive to alkaloids (Aerts *et al.* 1992; van Dam *et al.* 1995b). *Spodoptera exigua* thus served as a model for all generalist herbivores. We did not test specialist herbivores because they are not affected by PAs. Their presence does not influence optimal $A(x)$ at all and only reduces the relative growth of the plant with a constant (Iwasa *et al.* 1996).

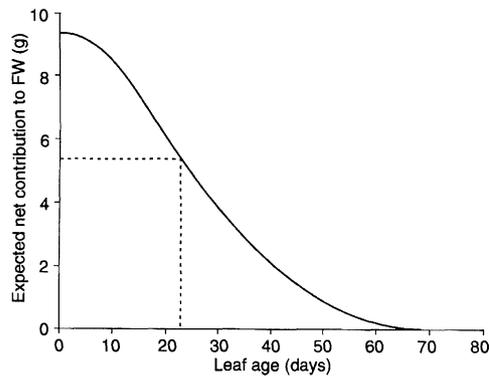


Fig. 2. Residual net contribution to plant fresh weight as a function of leaf age in *Cynoglossum officinale*. The dashed line indicates the age at which a leaf has produced its own fresh weight.

PAs were extracted from *C. officinale*, painted in different concentrations on lettuce leaf discs and tested in a no-choice situation as described in van Dam *et al.* (1995b). The range in PA concentrations covered the whole range as found in leaves of *C. officinale* (Van Dam *et al.* 1994). Herbivory on discs with PAs was expressed relative to herbivory on control discs (Fig. 3). Both equations (3) and (4) were fitted on the data (for results see legend to Fig. 3). Because the equations fitted equally well, they were both evaluated in the model.

For a reliable estimate of herbivory in the absence of PAs, h_0 , we should find or produce mutants of *C. officinale* whose PA biosynthesis is blocked, without affecting other plant characteristics. These mutants should then be placed under natural conditions. Because these mutants are not available, we roughly estimated h_0 as $0.1 \text{ gFW gFW}^{-1} \text{ day}^{-1}$. In the paper of Iwasa *et al.* (1996), very different values of h_0 , ranging from 0.08 to 0.4, were taken to examine their effect on model predictions but these changes did not have a great effect on the outcome of the model.

COSTS OF PRODUCTION OF LEAVES AND PAs

Based on combined measurements from leaves of field and laboratory-grown plants the average leaf weight was determined on 1 g FW. We realize that leaves of different ages do not all have the same weight but it simplifies matters considerably in the model. Moreover, the amount of PAs can thus be read directly as the concentration (mg.gFW^{-1}). Because we decided to express all parameters in units of FW, by definition the cost of producing a leaf, a , is 1 g FW.

In general, defences are thought to be costly, because their production, transport and storage divert resources from growth and reproduction (Coley 1985; Simms 1992). However, in a herbivore-free environment there was no significant negative genetic correlation between PA content and growth in rosette plants of *C. officinale* (van Dam & Vrieling 1994). This indicates that the production costs of PAs may

be too small to be measured under these circumstances. An experiment with *Senecio jacobaea*, another PA-containing plant species growing in the same habitat as *C. officinale*, showed that PAs are costly only under light-limiting conditions (Vrieling & van Wijk 1994). In the model we assume that there is a trade-off between production of biomass and PAs and that both productions are limited by the photosynthesis of the plant. Therefore, we estimated production costs of PAs relative to biomass.

Because not all enzymatic steps in the biosynthetic pathway of PAs are known yet (Hartmann & Witte 1994), we could not calculate the energy costs necessary for producing a PA exactly. Therefore, we used the construction costs of another alkaloid, nicotine, as an estimate. The costs for producing nicotine were estimated as $5.0 \text{ g CO}_2 \text{ g}^{-1}$ by Gulmon & Mooney (1986). The production costs of 1 g dry leaf biomass was estimated as 2.69 g CO_2 . Thus the production of 1 g alkaloid costs $5.0/2.69 = 1.85 \text{ g DW}$, which corresponds with 9.25 g FW . Therefore, the costs of 1 mg PA, b , is set to 0.00925 g FW , which should be considered as the minimum value for costs of PAs.

Results

Using the measured or estimated values listed in Table 1 and the hyperbolic $h(A)$ function, the model predicted a gradual decrease of alkaloids with leaf age (Fig. 4). On the other hand, with the exponential $h(A)$ function the model predicted that PAs stay relatively more constant with age and then suddenly drop to zero at the end of the leaf's life. Although both alternatives predict PA levels which are in the natural range for *C. officinale*, the shape of $A(x)$ corresponding with the hyperbolic $h(A)$ curve seems to be most in line with our *C. officinale* data (Fig. 4).

For a plant that is optimally allocating its PAs, the relative growth rate $r^* = 0.0311 \text{ day}^{-1}$, which is in the upper range of growth rates of *C. officinale* rosettes in the field (from 0.005 day^{-1} under natural, nutrient-

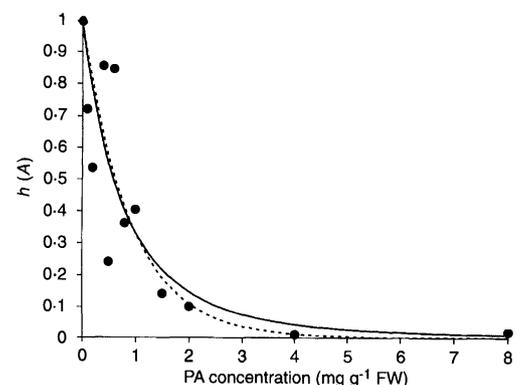


Fig. 3. Relative herbivory by *Spodoptera exigua* larvae as a function of pyrrolizidine alkaloid (PA) concentration, $h(A)$. Solid line: hyperbolic function, $h(A) = (1 + 0.375A)^{-3.46}$. Non-linear regression: $R^2 = 0.721$. Dashed line: exponential function, $h(A) = e^{-1.11A}$. Non-linear regression: $R^2 = 0.720$.

poor conditions in the sand dunes, to 0.069 day^{-1} under nutrient-rich conditions in an experimental garden; de Jong *et al.* 1987; Wesselingh 1995).

With the same parameter values, the accumulated herbivory on leaves is less than 10% until 60 days after emergence, after which it rises sharply to 46% at the end of the leaf's life, when it is left undefended (Fig. 5). Although this final value for leaf herbivory is higher than what we found in the field, the overall picture is the same: young leaves are less damaged than old leaves (van Dam 1995b).

In the sensitivity analysis we increased the value of each parameter by 10% to examine the effect on optimal $A(x)$, using the model with the hyperbolic $h(A)$ curve. Because changes in $A(0)$ always corresponded with changes in $A(x)$ (Iwasa *et al.* 1995), for simplicity we only considered $A(0)$ (Table 1).

Increasing the value for leaf production cost, a , resulted in a 6.7% increase of $A(0)$ (Table 1). Thus if leaves are more expensive, e.g. because it costs more energy to construct them, they should be better defended. Moreover, a higher value for f_{max} , the maximal net production, reflecting a more favourable and productive habitat for plant growth, resulted in lower optimal $A(0)$. $A(0)$ decreased considerably when the effectiveness of the defence, denoted by the values for c and k , was increased by 10%. Thus more effective PAs should be produced in smaller quantities. Changing one of the other parameters, including costs of alkaloid production, only slightly affected the value of $A(0)$.

Figure 4 also shows that the predicted PA levels for old leaves were still considerably higher than the values we measured in the field. A possible reason for this difference may be the overestimation of the photosynthetic activity of older leaves. Inherent to the method we used to determine the net production of individual leaves, the effect of shading on older leaves could not be measured. The linear relationship between age and net production as depicted in Fig. 1, thus may overestimate the value of $f(x)$ at higher leaf

ages. Therefore, we postulated an alternative mathematical function for $f(x)$ (Fig. 1, dotted line).

The shape of the predicted distribution of PAs indeed approximated the measured values more closely after incorporation of the non-linear function for $f(x)$ in the model (Fig. 6). However, the estimated PA levels were consistently too high. Because the values of both costs of PA production (b) and herbivory in absence of PAS (h_0) were estimated rather than measured, we changed these values. As shown in Table 1, a higher value for b and a lower value for h_0 both reduce PA levels. Doubling the value for b only slightly decreased $A(0)$ (see also Iwasa *et al.* 1996), whereas halving the value for h_0 gave a very good prediction for the PA distribution as we measured in field plants (Fig. 6). This best-fitting model resulted in lower predictions for r^* ($r^*=0.0161$ if $h_0=0.1$, and $r^*=0.0166$ if $h_0=0.05$), which is closer to the realized growth rates of *C. officinale* in the field (Wesselingh 1995).

Finally, we compared the r^* of allocating and non-allocating types with each other. For the non-allocating type we first calculated optimal A , which resulted in the highest r^* compared to other non-allocating types. In plants with a linear $f(x)$ (Fig. 1, solid line), the r^* of this non-allocating type was only 1.3% lower than in plants that optimally reallocate their defences. In slower growing plants with non-linear $f(x)$ (Fig. 1, broken line), no allocation resulted in a r^* that was 9.3% lower. This indicates that reallocation of defences is particularly advantageous in slow-growing plants, which commonly is the case for *C. officinale* plants growing under natural conditions.

Discussion

In this paper we made realistic predictions for the optimal PA distribution in exponentially growing rosette plants of *C. officinale*, assuming that the photosynthetic value of a leaf decreases with leaf age, herbivory decreases with increasing PA concentration and production of PAs is costly but reallocation is free.

Table 1. Description and values of the parameters in the model and sensitivity analysis with the hyperbolic $h(A)$ function. For the sensitivity analysis all values were increased by 10% and the effect on maximum relative growth rate, r^* (day^{-1}), and optimal pyrrolizidine alkaloid (PA) concentration (mg gFW^{-1}) at leaf age is 0 days, $A(0)$, was examined. With the initial values of all parameters $r^*=0.0311$ and $A(0)=7.90$; % change = the change of $A(0)$ relative to $A(0)$ with the initial values

Parameter	Description	Units	Initial Value	Sensitivity analysis		
				r^*	$A(0)$	% change
a	Cost leaf production	g FW	1	0.0274	8.43	6.71
b	Cost PA production	g FW mg^{-1}	0.00925	0.0309	7.69	-2.66
f_{max}	Maximal net production	gFW $\text{gFW}^{-1} \text{ day}^{-1}$	0.0685	0.0355	7.60	-3.80
h_0	Herbivory without PAs	gFW $\text{gFW}^{-1} \text{ day}^{-1}$	0.1	0.0310	8.14	3.04
x_l	Age at f_{max}	days	15.7	0.0305	7.94	0.51
x_{max}	Maximum leaf age	days	69	0.0329	7.77	-1.65
c	Effectiveness of PAs	mg^{-1}	0.375	0.0314	7.36	-6.84
k	Effectiveness of PAs	1	3.46	0.0316	7.05	-10.76

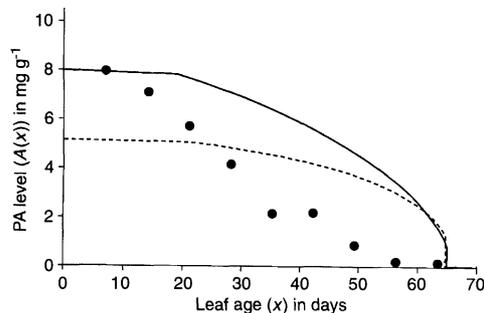


Fig. 4. Predicted optimal distribution of pyrrolizidine alkaloids in *Cynoglossum officinale* rosette plants. Parameter values are listed in Table 1. Solid line: hyperbolic function for $h(A)$, $r^*=0.0311 \text{ day}^{-1}$. Dashed line: exponential function for $h(A)$, $r^*=0.0326 \text{ day}^{-1}$. Closed circles: PA values for leaves of field plants (data taken from Fig. 2 in van Dam *et al.* 1994).

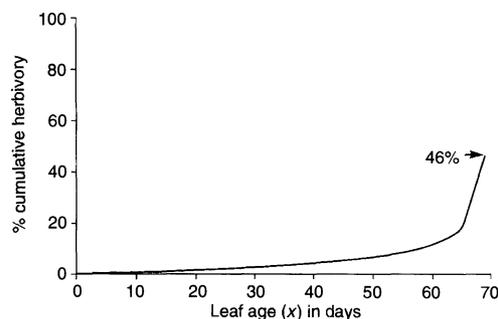


Fig. 5. Predicted cumulative herbivory on leaves of a *Cynoglossum officinale* rosette plant that is optimally allocating its PAs (solid line).

The decrease in net production with leaf age is caused by two mechanisms: senescence and overshadowing by younger leaves (Larcher 1975; Mooney & Gulmon 1982). Leaf senescence is a genetically determined process that may start shortly after maximal leaf expansion and leads to the hormonally controlled reallocation of resources to the youngest leaves (Thomas & Stoddard 1980; Chabot & Hicks 1982). Commensurate with this reallocation, the photosynthetic capacity of the ageing leaf declines, because the concentration of nitrogen and photosynthetic enzymes decreases (Larcher 1975). Shading may have an additional negative effect on the realized net production of ageing leaves.

By definition, measurements of photosynthetic capacity determine the maximal net rate of photosynthesis under optimal conditions with respect to all external factors, such as light intensity (Larcher 1975; Mooney *et al.* 1981). These measurements thus do not take into account that senescing leaves may be shaded by the newly emerged younger leaves. Therefore, the value of the older leaves to the plant may well be less than we initially calculated (Harper 1989). In our model we tried to take account of shading by introducing a non-linear function for $f(x)$. It would be interesting to actually quantify this assumption in the field.

The dose-dependent relationship between PA concentration and herbivory, $h(A)$, was determined with *S. exigua* larvae, which served as a model for all generalist herbivores. Other generalist herbivores, for example *Helix aspersa*, are less sensitive to high PA concentrations (van Dam *et al.* 1995b), which means that the $h(A)$ curve we used in the model might overestimate the effectiveness of PAs. Evaluation of our model with lower values for c and k , however, resulted in higher estimations for the PA concentration of each leaf over its whole life, without changing the shape of the curve (data not shown).

Moreover, we considered herbivory as a function of PA concentration only, while nitrogen and water levels also are important factors that determine the suitability of food for herbivores (Scriber 1984). Old leaves contain less nitrogen, mineral compounds and other nutrients than young leaves (de Jong *et al.* 1987; Harper 1989; van Dam *et al.* 1995b). This may explain the difference between the predicted accumulated herbivory on old leaves (46%, Fig. 5) and the observed level of damage ($\pm 10\%$, van Dam *et al.* 1995b) on the oldest leaves in the field. Since deterioration of leaf quality is age-dependent, herbivory could better be expressed as a function of defence level and age, $h(A, x)$ (Iwasa *et al.* 1996).

Regarding the assessment of PA production costs we met two problems. First, we could not measure or calculate costs of PA biosynthesis in *C. officinale* directly as was carried out for nicotine in tobacco (Gulmon & Mooney 1986). The inability to measure costs of chemical defence production made Zangerl & Bazzaz (1992) suggests that 'the cost, while real, is slight and therefore undetectable or biologically irrelevant'. Consequently, it has been hypothesized that 'ecological costs', for example, the deleterious effect of defences on the predators and parasites of herbivores, must be invoked to explain why not all plants have very high defence levels (Simms 1992). Contrary to this statement, the outcome of the model shows that the physiological costs of defences, even though they are very low for biologically relevant

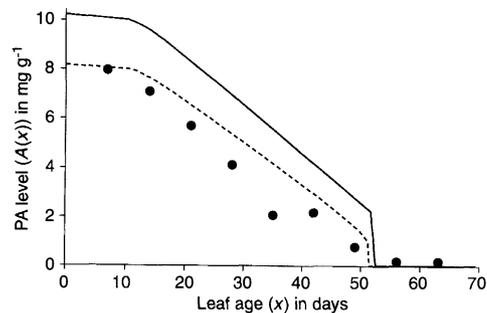


Fig. 6. Predicted optimal distribution of pyrrolizidine alkaloids in *Cynoglossum officinale* rosette plants, using a non-linear function for $f(x)$. Solid line: $h_0=0.1 \text{ day}^{-1}$, $r^*=0.0161 \text{ day}^{-1}$. Dashed line: $h_0=0.05 \text{ day}^{-1}$, $r^*=0.0166 \text{ day}^{-1}$. Closed circles: PA values for leaves of field plants (data taken from Fig. 2 in van Dam *et al.* 1994).

amounts when compared to leaf construction costs (Gulmon & Mooney 1986), may explain optimal defence patterns in plants without invoking ecological costs. Whether or not ecological costs for defence exist, remains an interesting issue. However, our model does not lend support to Simms' assertion that they *must* exist to predict realistic defence concentrations that fall in the range observed in nature.

Although we know that PAs are reallocated without losses from the old into the young leaves (van Dam 1995b), it is unknown how much energy this transport costs. Storage of PAs in vacuoles of *Senecio vulgaris* cells requires hydrolysis of ATP, indicating that the storage and probably also the release of PAs before transport, are energy requiring processes (M. Rickwärtz, personal communication). Transport costs may impose extra constraints to the redistribution of PAs. If the costs of transport are high, it will be advantageous to transport fewer PAs.

The selective value of reallocation of defences is higher in slow-growing plants, which is commonly the case for *C. officinale* rosettes growing in the sand dunes (Wesselingh 1995). In exponentially growing plants the number of new leaves formed per time unit will increase during the life span of a leaf. The PAs reallocated from an ageing leaf thus will constitute only a small fraction of the PAs needed for all the new leaves that are formed at the same time. Moreover, optimal A is higher in slow-growing plants. Reallocation of PAs thus will be more advantageous in these plants than in fast-growing plants with low A .

To make the mathematical calculation of the optimal schedule for $A(x)$ tractable, we assumed exponential growth for an indefinite period of time. Instead, leaves of *C. officinale* are only present from March to November, when they are killed by the first severe night frost. This encompasses a period of *c.* 270 days. As the generation time of a leaf is 69 days, only four generations of leaves can be formed and the fourth leaf probably dies before it is 69 days old. Iwasa & Roughgarden (1984) showed that usually the allocation schedule that realizes the fastest growth over an indefinite period, is also the one that maximizes reproductive success, even if the growth period is not very long. Similarly Yamamura & Tsuji (1995) showed that the optimal allocation to defense is constant and is not affected by the length of the growing season (their fig. 2C). Only during a short period at the end of the growing season, the optimal allocation to defense is less. This is because in their model only the amount of carbon, and not the amount of defense chemicals, can be transferred to reproduction.

When applying these results to our model, this implies that the optimal $A(x)$ for the first three generations of leaves produced is the same. We calculate this schedule correctly under the assumption of indefinite growth. Optimal $A(x)$ for the fourth generation of leaves may differ.

How it will differ depends on the efficiency at which carbon and alkaloids from the senescent leaves can be carried over to the next spring. We have no data on these processes in *Cynoglossum*. Thus optimal $A(x)$ in the last generation of leaves produced could differ from leaves produced earlier in the season but it could also be similar if, for instance, there is no reallocation from leaves with frost damage or when *Cynoglossum* is able to store alkaloids from these leaves in its tap-root in winter. Another concern may be that plants rarely grow exponentially. As plants grow, shading is expected to increase (in fact, Fig. 6 suggests that shading is important). On the other hand, growth of rosettes of *Cynoglossum* in an experimental garden was close to exponential from germination in spring until mid-August (de Jong *et al.* 1987). If plants grow slowly they should allocate more to defense (Table 1). Similarly, if the relative growth of a plant is high early in life and low late in life, it is optimal for a plant to allocate less to defense when young and more when old (discussed in Yamamura & Tsuji 1995). We would expect this result to hold when growth is not exponential. However, deviations from the exponential curve make our model untractable.

To enhance intelligibility of the model, we also made some simplifying assumptions with respect to the costs of leaf and PA production. First, we assumed that all leaves weighed 1 g FW. In reality, the very young leaves weigh less than fully expanded leaves. This means that the model probably underestimates the PA concentration during the first 2 weeks. Second, we settled all costs for leaf production at day 0. It seems more realistic that investments in leaf build-up are made over the whole period of leaf expansion (van Dam *et al.* 1994). This probably resulted in an overestimation of the value, and thus of the PA concentration, of very young leaves.

The model also gave some general predictions for a plant that allocates its chemical defences optimally: (1) the amount of defences decreases with leaf age; (2) if leaves are more expensive to construct they contain more defence substances; (3) defences are less favourable in environments which allow fast growth; (4) the concentration of defence substances is lower if they are more effective.

The last three predictions are in line with the resource availability theory (Coley *et al.* 1985; Coley 1988). This theory predicts that slow-growing plants that are adapted to resource-poor environments, e.g. shading, have higher amounts of defences. In slow-growing species, allocation of resources to defence production does not result in as great a reduction of growth as in fast growing plants. In the same way we found that an increase of leaf cost, a , results in slower growth and thus in more defence substances (Table 1). The increase in defence will even be greater if we consider the fact that leaves on slow-growing plants generally live longer (Coley 1988) and have a lower maximal photosynthetic capacity (Chabot & Hicks

1982). In our model, both an increase of x_{max} and a decrease of f_{max} lead to an increase in the levels of defence substances. Likewise, we predict that the levels of defence substances will decrease if f_{max} is high, thus in resource-rich environments that allow fast growth.

Finally, we also predict that a plant should produce less defence chemicals if these are more effective. In the classical defence theories a distinction is made between qualitative (or mobile) and quantitative (or immobile) defences (Feeny 1976; Coley *et al.* 1985). The first would be very effective against herbivores in small concentrations, less expensive to produce and easy to reallocate. In accordance with these theories, our model also predicts that more effective defences should be produced in smaller amounts than less effective defences. Although this result seems obvious, the opposite (the more effective the defence, the more should be produced) might hold in other parts of the parameter space, especially at very low effectiveness of the defence chemical and high herbivory pressures relative to growth rate (Yamamura & Tsuji 1995).

As mentioned in van Dam *et al.* (1994) the PA distribution in *C. officinale* rosettes is quite extreme. Although we used *C. officinale* data, the model is general enough to apply to other species, because both effectiveness and costs of defences can be adjusted at will. Because we assumed that the defences were transported easily, it is more compatible with qualitative defences (Coley *et al.* 1985). However, in the context of the model, the difference between qualitative and quantitative defences is small and should vanish altogether if the model is extended to include transport costs as well.

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References

- Aerts, R.J., Stoker, A., Beishuizen, M., Jaarsma, I., van de Heuvel, M., van der Meijden, E. & Verpoorte, R. (1992) Detrimental effects of *Cinchona* leaf alkaloids on larvae of the polyphagous insect *Spodoptera exigua*. *Journal of Chemical Ecology* **18**, 1955–1964.
- Bazzaz, F.A. (1984) Demographic consequences of plant physiological traits: some case studies. *Perspectives on Plant Population Ecology* (eds R. Dirzo & J. Sarukan), pp. 324–346. Sinauer, Sunderland.
- Chabot, B.F. & Hicks, D.J. (1982) The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**, 229–259.
- Charlesworth, B. (1980) *Evolution in age-structured populations*. Cambridge University Press, Cambridge.
- Coley, P.D. (1988) Effect of plant growth and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* **74**, 531–536.
- Coley, P.D., Bryant, J.P. & Chapin III, F.S. (1985) Resource availability and plant anti-herbivore defense. *Science* **230**, 895–899.
- Cranshaw, W.S. & Radcliffe, E.B. (1980) Effect of defoliation on yield of potatoes. *Journal of Economic Entomology* **73**, 131–134.
- van Dam, N.M. (1995) *Production, distribution, and function of secondary metabolites. A case study on pyrrolizidine alkaloids in Cynoglossum officinale*. Thesis, Leiden University.
- van Dam, N.M. & Vrieling, K. (1994) Genetic variation in constitutive and inducible pyrrolizidine alkaloid levels in *Cynoglossum officinale* L. *Oecologia* **99**, 374–378.
- van Dam, N.M., Verpoorte, R. & van der Meijden, E. (1994) Extreme differences in alkaloid levels between leaves of *Cynoglossum officinale* L. *Phytochemistry* **37**, 1013–1016.
- van Dam, N.M., Witte L., Theuring, C. & Hartmann, T. (1995a) Distribution, biosynthesis and turnover of pyrrolizidine alkaloids in *Cynoglossum officinale* L. *Phytochemistry* **39**, 287–292.
- van Dam, N.M., Vuister, L.W.M., Bergshoeff, C., de Vos, H. & van der Meijden, E. (1995b) The 'raison d'être' of pyrrolizidine alkaloids in *Cynoglossum officinale*: deterrent effects against generalist herbivores. *Journal of Chemical Ecology* **21**, 507–523.
- Feeny, P. (1976) Plant apparency and chemical defense. *Biochemical Interactions Between Plants and Insects* (eds J. W. Wallace & R. L. Mansell), pp. 1–40. Plenum, New York.
- Gulmon, S.L. & Mooney, H.A. (1986) Costs of defence and their effects on plant productivity. *On the Economy of Plant Form and Function* (ed. T. J. Givnish), pp. 681–698. Cambridge University Press, Cambridge.
- Harper, J. (1989) The value of a leaf. *Oecologia* **80**, 53–58.
- Hartmann, T. & Witte, L. (1994) Chemistry, biology and chemoeology of the pyrrolizidine alkaloids. *Alkaloids: Chemical and Biological Perspectives*, vol. 9 (ed. S. W. Pelletier), in press. Pergamon Press, Oxford.
- Iwasa, Y. & Roughgarden, J. (1984) Shoot/root balance: optimal growth of a system with many vegetative organs. *Theoretical Population Biology* **25**, 78–105.
- Iwasa, Y., Kubo, T., van Dam, N.M. & de Jong, T.J. (1996) Optimal level of chemical defense decreasing with leaf age. *Theoretical Population Biology*, **50**, in press.
- Janzen, D.H. (1979) New horizons in the biology of plant defences. *Herbivores: Their Interaction with Secondary Plant Metabolites* (eds G. A. Rosenthal & D. H. Janzen), pp. 331–350. Academic Press, New York.
- de Jong, T.J., Klinkhamer, P.G.L. & Prins, A.H. (1986) Flowering behaviour of the monocarpic perennial *Cynoglossum officinale* L. *New Phytologist* **103**, 219–229.
- de Jong, T.J., Klinkhamer, P.G.L., Nell, H.W. & Troelstra, S.R. (1987) Growth and nutrient accumulation of the biennials *Cirsium vulgare* and *Cynoglossum officinale* under nutrient-rich conditions. *Oikos* **48**, 62–72.
- de Jong, T.J., Klinkhamer, P.G.L. & Boorman, L.A. (1990) Biological flora of the British Isles. *Cynoglossum officinale* L. *Journal of Ecology* **78**, 1123–1144.
- Jurik, T.W. & Chabot, B.F. (1986) Leaf dynamics and profitability in wild strawberries. *Oecologia* **69**, 296–304.
- Krishik, V.A. & Denno, R.F. (1983) Individual, population, and geographical patterns in plant defense. *Variable Plants and Herbivores in Natural and Managed Systems* (eds R. F. Denno & M. S. McClure), pp. 463–512. Academic press, New York.

- Larcher, W. (1975) *Physiological Plant Ecology*. Springer Verlag, Berlin.
- McKey, D. (1974) Adaptive patterns in alkaloid physiology. *American Naturalist* **108**, 305–320.
- Mooney, H.A. & Gulmon, S.L. (1982) Constraints on leaf structure and function in reference to herbivory. *BioScience* **32**, 198–206.
- Mooney, H.A., Field, C., Gulmon, S.L. & Bazzaz, F.A. (1981) Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. *Oecologia* **50**, 109–112.
- Poorter, H., Remkes, C. & Lambers, H. (1990) Carbon and nitrogen economy of 24 wild species differing in growth rate. *Plant Physiology* **94**, 621–627.
- Sackston, W.E. (1959) Effects of artificial defoliation on sunflowers. *Canadian Journal of Plant Science* **39**, 108–118.
- Scriber, J.M. (1984) Host plant suitability. *Chemical Ecology of Insects* (eds W. J. Bell & R. T. Caidé), pp. 159–202. Sinauer, Sunderland.
- Simms, E.L. (1992) Costs of plant resistance to herbivory. *Plant resistance to Herbivores and Pathogens* (eds S. Fritz & E. L. Simms), pp. 363–391. The University of Chicago Press, Chicago.
- Stearns, S.C. (1992) *The Evolution of Life-History Strategies*. Oxford University Press, Oxford.
- Thomas, H. & Stoddard, J.L. (1980) Leaf senescence. *Annual Review of Plant Physiology* **31**, 83–111.
- Vrieling, K. & van Wijk, C.A.M. (1994) Cost assessment of pyrrolizidine alkaloids in ragwort (*Senecio jacobaea* L.). *Oecologia* **97**, 541–546.
- Wesselingh, R.A. (1995) *Ecology and genetics of reproductive timing in facultative biennial plants*. Thesis, Leiden University.
- Yamamura, N. & Tsuji, N. (1995) Optimal strategy of plant herbivore defense: implication for apparency and resource availability theory. *Ecological Research* **10**, 19–30.
- Zangerl, A.R. & Bazzaz, F.A. (1992) Theory and pattern in plant defense allocation. *Plant Resistance to Herbivores and Pathogens* (eds S. Fritz & E. L. Simms), pp. 363–391. The University of Chicago Press, Chicago.

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