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Biomass partitioning and its effect on reproduction in a monocarpic perennial (*Anthriscus sylvestris*). Response to nitrogen and light supply

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SUMMARY

Plants of *Anthriscus sylvestris* (L.) Hoffm. originating from seed were grown from April 1989 to June 1990 in a factorial pot experiment to study the effects of light and nitrogen over time on biomass allocation to different plant parts and their relation to reproduction and reproductive effort. For a species depending on resources stored in a taproot for flowering, it was expected that environmental conditions promoting allocation to roots would lead to a high reproductive output and/or reproductive effort. In this context the relation between growth of the resource-storing taproot and the resource-capturing side-roots was studied. The first year, during the vegetative stage, the root/shoot ratio was influenced by an interaction between light and nitrogen, and within the root fractions the two components were equally affected. During the flowering stage, the variation in partition pattern was mainly time related. It was found that sexual reproductive output varied in direct proportion to the amount of resources stored in the taproot during the vegative phase of the plant. Despite the large variation in root/shoot ratio during the first growing season, this factor had no influence on the reproductive effort, i.e. seed production was determined by plant size, which depended on resources stored in the taproot at the end of the first growing season and on the availability of nitrogen in the second growing season.

Key-words: reproductive effort, root/shoot ratio, resource storage.

INTRODUCTION

Anthriscus sylvestris L. (Hoffm) is a facultative biennial that shows a size-dependent flowering. Plants have to reach a minimum size in the autumn for vernalization to occur. During the year that the plants flower, resources stored in the taproot are used in the formation of the flowering plant (Lang *et al.* 1976; Imhoff & Kühbauch 1980). Therefore, reproductive output depends on the resource allocation pattern during the rosette stage, especially with respect to partitioning between root and shoot. The species can also reproduce vegetatively by producing side rosettes in connection with the main taproot.

In general, the root/shoot ratio of herbaceous species decreases with age and size (Wilson 1988). However, this is not true for root crops which store resources in their taproot (Ford & Thorne 1967; Hole *et al.* 1984). Currah & Barnes (1979) analysed this for carrot. They found that the partitioning between root and shoot depended on age rather than on size and that early in development the root/shoot ratio decreases, but beyond a certain age it starts to increase. The mechanism behind this behaviour remains unclear.

All plants are able to modify their basic partitioning pattern to some extent in response to environmental conditions. Photosynthesis and nutrient availability are important determinants of dry matter partitioning between root and shoot, among other factors. It is well known that changes in light intensity and nutrient supply cause shifts in the relative allocation to above- and below-ground parts (reviewed by Brouwer 1962; Wilson 1988, among others). Results of empirical studies support general predictions that factors such as resource availability will influence the partitioning of resources between reproduction versus vegetative growth. Although most research has focused on plant responses and adaptations to single features in the environment, plants in nature encounter multiple stresses (Chapin *et al.* 1987). Lovett-Doust (1981) showed that as levels of light and nitrogen decrease, these two factors interact to induce a shift from generative to vegetative reproduction in *Ranunculus repens* L. Similar interacting effects on reproductive strategy have been reported for species with clonal growth by Van Baalen *et al.* (1990) and Powelsson & Lieffers (1992).

The objectives of this study were to determine how light and nitrogen, as well as their interactions over time affected biomass partitioning, reproductive allocation and reproductive effort in *A. sylvestris*. I expected that environmental conditions promoting allocation to roots the first year would lead to higher reproductive output and/or reproductive effort. In this context there was a need to explore the relation between growth of the resource-storing taproot and that of the resource-capturing side roots, and to relate reproductive output to the growth of different plant parts before vernalization.

METHODS

Growth conditions and plant material

Seedlings of *A. sylvestris* were collected in late April 1989 from a dense carpet of seedlings at a natural site south of Uppsala in central Sweden. Each seedling was planted individually in a 3-l pot containing inert sand and placed outdoors in a netting enclosure at Ultuna, south of Uppsala in central Sweden (59°58′N, 17°35′E). After a period of acclimation, 224 individuals of about the same size were chosen for the experiment. Half the plants were harvested during 1989. At the end of the first growing season, the remaining plants were kept in a sand bed during winter where they were exposed to normal winter conditions. Early in April, before growth had started, the pots were transferred back to the netting enclosure. During periods of rainfall the plants were covered with plastic sheets. The plants were treated with fungicides on two occasions, and on two other occasions an insecticide had to be used to control aphids.

Treatments

Altogether, there were four treatments: (1) high light–high nitrogen availability, (2) high light–low nitrogen availability, (3) low light–high nitrogen availability and (4) low light–low nitrogen availability.

The intensity of the high irradiance treatment was 40% of that of natural light, while in the low irradiance treatment the corresponding value was about 10%. The light level was manipulated by placing wooden frames covered with layers of burlap of various thickness over the plants.

Fertilizer was supplied every second day as a nutrient solution (cf. Ingestad & Lund 1979, Table 2 exp. 1–15, 21). In total, each plant received 100 mg N per year in the high-N treatment and 20 mg N per year in the low-N treatment. The nitrogen was added in amounts based on the calculated needs of the plant, which growth was assumed to fit in an S-shaped growth model (Ingestad & Ågren 1984). All other nutrients were added in free access. The pots were watered to saturation on days when fertilizer was not added.

Sampling

Seven harvests were made during the first growing season, at 9-day intervals, starting on 28 June 1989. Four plants in each treatment were harvested randomly, and the remaining pots were rearranged on every harvest occasion. The plants were separated into leaf, taproot and fine-root fractions, dried for 24 hours at 105°C and weighed.

During the second growing season six harvests were made, in the same way and at the same intervals as during the first year, starting on 18 May 1990. At this time the plants were flowering and seed setting had begun. Each plant was separated into two fractions: the flowering main plant and the vegetative side rosettes connected to the main plant. The main plant was then divided into biomass allocated to generative reproduction (flowers and seeds, both including pedicels), stalk, leaves, taproot and side roots. The vegetative rosettes were separated into leaves and roots. All plants were then dried and weighed as described above.

Calculations

Reproductive effort was calculated as the biomass of generative parts divided by the total biomass of the main plant. To examine the relation between growth of the taproot and that of the side roots the ratio between the two was calculated. The root/shoot ratio was calculated by dividing the weight of below-ground plant parts by the weight of above-ground parts. All calculations were based on dry weights.

Each plant was considered as a replicate. A three-factorial analysis of variance was used and followed in some cases by an LSD test with the critical level of significance set at 0·05. The SAS procedure GLM was used to perform the analyses (SAS Institute Inc. 1982). A regression analysis was made to test the correlation between seed weight and taproot biomass (first growing season, last harvest) and between seed weight and total plant biomass (as above).

RESULTS

First growing season

Nitrogen addition rate and light level interacted significantly in their effects on the plant parameters (Table 1). Thus the effect of nitrogen on total biomass and on allocations to side roots and taproot were significantly dependent on light level. In general, biomass production was highest in the treatments where the availability of both resources was high. When light, but not nitrogen, was reduced, the weights were reduced by 50% for

Table 1. Interaction effects on biomass allocation to different plant parts and root/shoot ratio (RSR), first growing season. N=nitrogen, L=light, T=time. *=$P<0{\cdot}05$, **=$P<0{\cdot}01$, ***=$P<0{\cdot}001$, NS=not significant. *F*-values and degrees of freedom are shown (d.f.)

	d.f.	Plant weight	Taproot	Side roots	Leaves	RSR
N × L	1	13·66***	18·68***	22·48***	1·65NS	28·50***
N × T	6	13·37***	7·77***	9·60***	19·45***	4·31NS
L × T	6	0·88NS	0·68NS	1·35NS	2·15NS	1·71NS
L × N × T	6	1·03NS	0·64NS	2·07NS	1·88NS	1·63NS

Table 2. Mean taproot weight, mean plant weight (g) and root/shoot ratio (RSR), the first growing season, in relation to light and nitrogen supply level ± standard error ($n=28$). Means followed by the same letter are not significantly different. N=high nitrogen supply, n=low nitrogen supply, L=high light level, l=low light level

Resource availability	Taproot	Plant weight	RSR
NL	0·54 ± 0·04a	1·33 ± 0·17a	1·55 ± 0·09a
Nl	0·28 ± 0·03b	0·88 ± 0·06b	0·67 ± 0·05b
nL	0·12 ± 0·03c	0·26 ± 0·03c	2·11 ± 0·12c
nl	0·17 ± 0·02c	0·34 ± 0·02c	1·79 ± 0·12a

the taproot and 66% for total biomass compared with the high N/high light treatment (Table 2). By contrast, leaf weight was not affected by light intensity (Table 1) which resulted in a decrease of the root/shoot ratio. In the low-N treatments reductions in the biomass of the various fractions were about proportional to the reduction in the resource. At high light level taproot biomass and plant weight were smaller compared with the low light treatment, although not significant (Table 2), i.e. the light level had no effect in combination with the low-N treatment.

The root/shoot ratio varied between 0·5 and 2·7 (Fig. 1). As can be seen, there were already differences between the treatments at first harvest; thus it is unclear how quickly the adjustment to the different environmental conditions occurred. Differences in root/shoot ratios between treatments remained about the same throughout the experiment, indicating that the resource ratios (light/nitrogen availability) were stable during the period.

The interaction between light and nitrogen in their effects on root/shoot ratio suggests that the response to light depends on the availability of nitrogen and vice versa (Table 2). When the availability of both resources was high (NL) or low (nl) no significant difference was found between the two root/shoot ratios. Allocation to above-ground parts was highest in the high N/low light treatment and lowest in the low N/high light treatment.

The relation between taproot biomass and side-root biomass was unaffected by the treatments ($P=0{\cdot}105$ for the model), indicating that the root fractions responded as a unit.

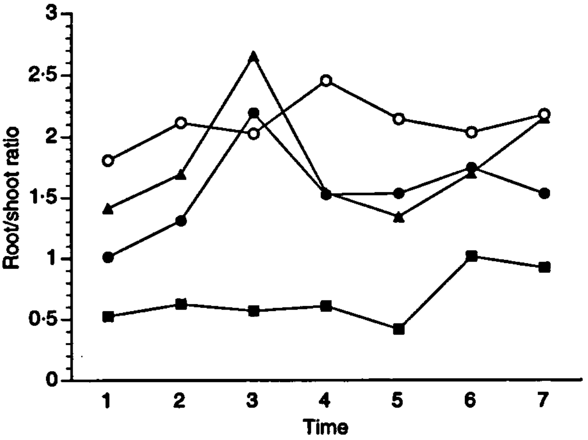

Fig. 1. Mean root/shoot ratio in relation to time and the availability of light and nitrogen, first growing season (n=4). First harvest on 28 June 1989. Nine days between harvests. Open circles=low N and high light availability, triangles=low N and low light availability, filled circles=high N and high light availability, squares=high N and low light availability.

Second growing season

The effects of main factors are presented in Table 3. Light and nitrogen interacted in the same way in their effect on allocation to all studied plant parameters as first growing season, except for side roots (Table 3). A second-order interaction was found for taproot biomass. In the high N/high light treatment taproot biomass increased early in the season but decreased thereafter. In the other treatments taproot weight did not increase initially. Instead, it tended to decrease until the last harvest, whereafter it increased in connection with seed ripening. However, the increase was only significant in the high N/high light treatment (Fig. 2).

Of the two-factor interactions, that between light and nitrogen had the most influence on plant growth. Seed biomass production was highest in the high N/high light treatment. At the lower light level seed production was only about half as high, and when nitrogen was reduced to 20% of the high level, seed weights were reduced by about the same magnitude (Table 3). By contrast, light and nitrogen did not interact in their effects on reproductive effort or root/shoot ratio (Table 4). Moreover, in contrast to the first year, variation in RSR was mainly time related (Fig. 3).

Not surprisingly, reproductive effort significantly changed with time. At the end of the experimental period about 13% of the biomass was invested in sexual reproduction which is in accordance with an earlier study (Hansson 1994). Furthermore, the high nitrogen treatment resulted in a slightly higher percentual allocation to reproduction (13% ± 0·8 resp 11 ± 1·0), whereas light had no effect. Nor did light and nitrogen interact in their effects on the relative allocation to sexual reproduction, suggesting that plant size determined reproductive output (Table 3). The only large allocation to side-rosettes occurred in the high N/high light treatment (Table 3).

Reproductive output versus biomass production and partitioning during the first season

One of the objectives of this study was to relate seed production to growth in the biomass of various plant parts during the vegetative phase. In this context, taproot size and total plant weight were the variables of interest. It was found that reproductive

Table 3. Effects of nitrogen, light and time and their interaction on biomass allocation to different plant parts, root/shoot ratio (RSR) and reproductive effort (RE), second growing season. N=nitrogen, L=light, T=time. *=P<0·05, **=P<0·01, ***=P<0·001, NS=not significant. F-values and degrees of freedom are shown (d.f.)

	d.f.	Plant biomass	Leaves	Stalk	Tap-root	Side-root	Gen. repr.	Veg. repr.	RSR	RE
N	1	162·98***	79·25***	160·56***	80·68***	57·44***	110·39***	5·07**	7·18*	5·31*
L	1	75·51***	1.82NS	48·23***	44·05***	52·81***	35·30***	3·02NS	10·77*	2·12NS
T	5	4·71**	1·47NS	7·35***	27·00***	2·09NS	14·88***	0·72NS	6·87***	14·33***
N × L	1	45·65***	1·41NS	33·85***	8·12***	21·74***	30·98***	3·62NS	0·29NS	0·92NS
N × T	5	1·33NS	0·73NS	1·56NS	2·02NS	0·84NS	3·13*	0·45NS	0·19NS	1·28NS
L × T	5	1·30NS	1·58NS	1·53NS	2·14NS	0·68NS	2·47*	0·71NS	0·15NS	0·65NS
N × L × T	5	1·45NS	1·80NS	0·99NS	2·55*	0·65NS	1·40NS	0·47NS	0·36NS	1·10NS

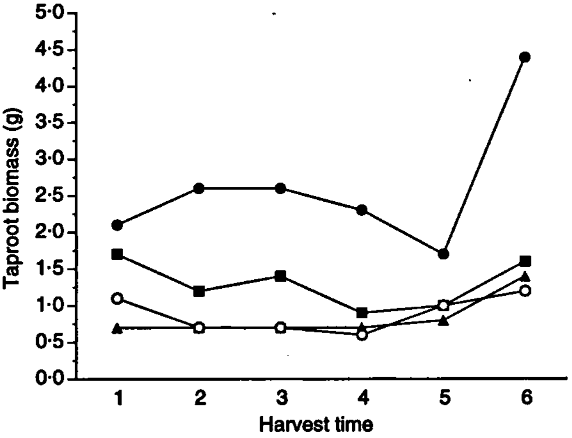

Fig. 2. Mean tap root weight in relation to time and the availability of light and nitrogen, second growing season ($n=4$). First harvest on 18 July 1990. Nine days between harvests. Open circles=low N and high light availability, triangles=low N and low light availability, filled circles=high N and high light availability, squares=high N and low light availability.

Table 4. Mean biomass allocated to generative reproduction, total reproduction and plant biomass (g) in relation to light and nitrogen supply level ± standard error ($n=24$), second growing season. Means followed by the same letter are not significantly different. N=high nitrogen supply, n=low nitrogen supply, L=high light level, l=low light level

Resource availability	Seed weight	Total reproduction	Plant biomass
NL	1·05 ± 0·11a	1·75 ± 0·16a	9·44 ± 0·56a
Nl	0·54 ± 0·04b	0·60 ± 0·06b	4·73 ± 0·18b
nL	0·26 ± 0·03c	0·26 ± 0·03c	2·90 ± 0·22c
nl	0·31 ± 0·03c	0·31 ± 0·03c	2·78 ± 0·18c

output was positively correlated with taproot biomass at the end of the first growth season ($P=0·04$), whereas the correlation with plant biomass was weaker ($P=0·08$) (Fig. 4a,b).

DISCUSSION

The present study shows that seed production by *A. sylvestris* was proportional to the amount of resources stored in the taproot during the vegetative phase. Moreover, taproot responded to environmental stress in the same way as the side-roots. Environmentally induced variation in biomass allocation is frequently discussed in terms of root/shoot ratio. Generally, the allocation to roots increases when plants are exposed to a scarcity of nutrients (Chapin 1980). It is claimed that this response improves the plants' ability to compete for the limiting resource because the organs receiving the increased allocation are involved in resource uptake. Similarly, when light is growth limiting, the allocation to leaves increases at the expense of root growth. However, the mechanism behind the partitioning between root and shoot is poorly

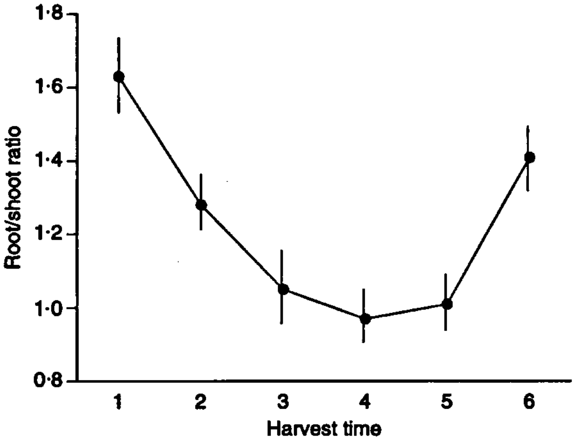

Fig. 3. Mean root/shoot ratio in relation to time, second growing season ($n=16$). First harvest on 18 July 1990. Nine days between harvests. Bars ± standard error.

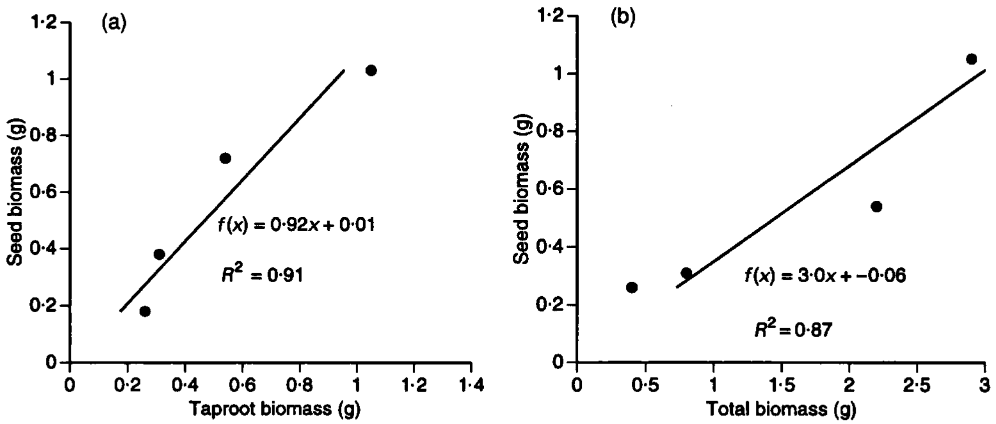

Fig. 4. Correlation between seed biomass and taproot biomass (a) and total plant biomass (b) at the end of the first growing season. The calculated regression lines are shown.

understood. Some claim that sucrose is central to the regulatory process (Farrar 1992), whereas others argue that plant hormones like cytokinins play a role (Kuiper *et al.* 1988; Wagner & Beck 1993). Since taproot is not primarily involved in resource uptake it cannot be assumed that the response of the taproot is related directly to the root/shoot ratio. Nevertheless, in *A. sylvestris* taproot growth and the root/shoot ratio showed the same response pattern and, as a consequence, factors influencing the root/shoot ratio might be critical for the reproductive success of the species. During the rosette phase this parameter was largely determined by the interaction between light and nitrogen, and it was possible to obtain ratios differing up to 5-fold. The plastic response was more pronounced at the high-N level, which suggests that *A. sylvestris* can compete for light more strongly at high levels of nitrogen availability than at lower levels. It can be assumed that plant growth was close to optimum when the supplies of both resources were high. The taproot also reached its largest biomass in this treatment (NL). The root/shoot ratio, when supplies of both resources were high (NL), was about the same as that obtained when both were limited (nl) in accordance with the predictions of the partitioning model of Hunt & Nicholls (1986). One of their main assumptions was that when plants are exposed to opposing stresses of equal strength the partioning ratio will not change owing to a balancing effect. Under low light conditions the difference in taproot size between the high- and low-N treatments was proportional to the difference in N availability between these treatments. The largest deviation from the root/shoot value at high resource availability (NL) was found in the treatment where only light was limiting (Nl). In this case relatively more biomass was allocated to leaves in order to acquire the most limiting resource (light), resulting in a cost for nitrogen uptake. Not all applied nitrogen was utilized in this treatment (Table 2) and, as a consequence, taproot growth was reduced. By contrast, the variation in root/shoot ratio during the flowering stage was strictly of temporal nature (Fig. 3), indicating that resources stored in the taproot are crucial for growth and are more important than resource imbalances in the environment. The large environmentally induced variation in RSR during the vegetative stage in the life cycle might have consequences on the generation time of the species, i.e. under poor conditions flowering will be delayed. One might conclude that juveniles are more sensitive to environmental stress, which agrees with the general view that the juvenile stage of the life cycle is important in determining the patterns of occurrence and relative abundance of adults (Grubb 1977; Harper 1977; Grime 1979).

Despite the large variation in root/shoot ratio during the first growing season, this factor had no influence on reproductive effort; i.e. seed production was determined by plant size, which depended on storage size at the end of the first growing season. The allocate stream is directed upwards until seed ripening (Imhoff & Kühbauch 1980), therefore two processes might explain the correlation between taproot size and reproductive output. First, a large taproot results in high remobilization of compounds to leaves leading to higher photosynthetic capacity which will be invested in seeds; secondly, a large taproot provides more compounds for seed production than a small.

The relative allocation to seeds was higher at the high level of nitrogen availability than at the lower level. In addition, side-rosettes only formed in the high-N treatments. This agrees with the finding of an earlier study where extra nitrogen fertilization enhanced the formation of axillary buds, i.e. clonal growth (Hansson 1994), which suggests that plants secure the resource required for sexual reproduction before investing in clonal growth. Such a reproductive strategy can be viewed as an adaptation to the intermittently disturbed and open vegetation types in which biennials often occur (Holt 1972; Grime 1988). The tendency to shift over to clonal growth, i.e. towards a perennial strategy, at high levels of nitrogen availability increases the number of potential habitats available for successful colonization and survival. This response might partly account for the reported increase in the abundance of *A. sylvestris* in nitrogen-enriched environments (Van Mierlo & van Groenendael 1991; Hansson & Persson 1994).

It can be concluded that the sexual reproductive output varies in direct proportion to the amount of resources stored in the taproot during the vegetative phase of the plant. Storage size was determined by an interaction between light and nitrogen availability, apparently driven by the need to maximize resource utilization and supporting the view that biomass partitioning is a growth-optimizing process (Chapin *et al.* 1987).

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REFERENCES

Brouwer, R. (1962): Distribution of dry matter in the plant. *Neth. J. Agric. Sci.* **10:** 399–408.

Chapin, F.S. (1980): The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* **11:** 233–267.

Chapin III, F.S., Bloom, A.J., Field, C.B. & Waring, R.H. (1987): Plant responses to multiple environmental factors. *BioScience,* **37:** 49–57.

Currah, I.E. & Barnes, A. (1979): Vegetable plant part relationships. I. Effects of time and population density on the shoot and storage root weights of carrot (*Daucus carota* L.). *Ann. Bot.* **43:** 475–486.

Farrar, J.F. (1992): The whole plant: carbon partitioning during development. In: *Carbon Partitioning Within and Between Organisms,* pp. 163–179, Farrar, C.J.J.F. & Gordon, A.J. (eds): Bio Science Publishing, Oxford.

Ford, M.A. & Thorne, G.N. (1967): Effect of CO_2 concentration on growth of sugar-beet, barley, kale and maize. *Ann. Bot.* **31:** 629–644.

Grime, J.P. (1979): *Plant Strategies and Vegetation Processes,* John Wiley, Chichester.

Grime, J.P. (1988): *Comparative Plant Ecology,* Unwin Ltd, London.

Grubb, P.J. (1977): The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Camb. Phil. Soc.* **52:** 107–145.

Hansson, M.L. (1994): Response of *Anthriscus sylvestris* (L.) Hoffm. to defoliation and different nitrogen supply levels. *Swedish J. Agric. Res.* **24:** 21–29.

Hansson, M.L. & Persson, T.S. (1994): *Anthriscus sylvestris* (L.) Hoffm. a conservation problem? *Ann. Bot. Fenn.* **31:** 205–213.

Harper, J.L. (1977): *Population Biology of Plants,* Academic Press, London.

Hole, C.C., Thomas, T.H., Barnes, A., Scott, P.A. & Rankin, W.E.F. (1984): Dry matter distribution between shoot and storage root of carrot, parsnip, radish and red beet. *Ann. Bot.* **53:** 625–631.

Holt, R. (1972): Effect of arrival time on recruitment, mortality and reproduction in successional plant communities. *Ecology* **53:** 668–673.

Hunt, R. & Nicholls, A.O. (1966): Stress and the coarse control of growth and root-shoot partitioning in herbaceous plants. *Oikos* **47:** 149–158.

Imhoff, H. & Kühbauch, W. (1980): Die verteilung von C14 Assimilaten in Wiesenkerbel (*Anthriscus sylvestris* L.) und Bärenklau (*Heracleum sphondylium* L.) in verschiedenen Entwicklungsstadien und Termine für eine wirkungsvolle Herbizidanwendung. *Zeitschr. Acker Pflanz.* **149:** 35–45.

Ingestad, T. & Ågren, G.I. (1984): Fertilization for long-term maximum production. In: Perttu, K. (ed.): *Ecology and Management of Forest Biomass Production Systems Dept. Ecol. & Environ. Res. Swed. Univ. Agric. Sci. Rep.* **15:** 155–165.

Ingestad, T. & Lund, A. (1979): Nitrogen stress in birch seedlings. *Physiol. Planta.* **45:** 137–148.

Kuiper, D., Shuit, J. & Kuiper, P.J.C. (1988): Effects of internal and external cytokinin concentrations on root growth and shoot to root ratio of *Plantago major* ssp. *pleiosperma* at different nutrient conditions. *Plant Soil* **111:** 231–236.

Lang, V., Kühbauch, W., Voigtländer, G. & Imhoff, H. (1976): Wanderung von C14-Assimilaten im Wiesenkerbel (*Anthriscus silvestris* (L.) Hoffm.). *Zeitschr. Acker Pflanz.* **143:** 287–293.

Lovett-Doust, L. (1987): Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). III. Response to light and nutrient supply. *J. Ecol.* **75:** 555–568.

Powelson, A.R. & Lieffers, V.J. (1992): Effects of light and nutrients on biomass allocation in *Calamagrostis canadensis. Ecography* **15:** 31–36.

Van Baalen, J., Ernst, W.H.O., Van Andel, J., Janssen, D.W. & Neilssen, H.J.M. (1990): Reproductive allocation in plants of *Scrophularia nodosa* grown at various levels of irradiance and soil fertility. *Acta. Bot. Neerl.* **39:** 183–196.

Van Mierlo, A. & Van Groenendael, J. (1991): A population dynamic approach to the control of *Anthriscus sylvestris* (L.) Hoffm. *Ecography* **15:** 31–36.

Wagner, B.M. & Beck, E. (1993): Cytokinins in the perennial herb *Urtica dioica* L. as influenced by its nitrogen status. *Planta* **190:** 511–518.

Wilson, J.B. (1988): A review of evidence on the control of shoot:root ratio, in relation to models. *Ann. Bot.* **61:** 433–449.