

The carbon economy and ecological strategy of Yarrow (*Achillea millefolium* L.)

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Summary

Yarrow (*Achillea millefolium* L.) is a perennial competitive ruderal that reproduces both vegetatively from rhizomes and from seed. Originally introduced into New Zealand as a pasture species, yarrow has become an increasing problem on arable and horticultural land. The growth and carbon economy of individual plants established from rhizome fragments was studied from December 1987 until January 1990. After June 1988 rhizomes were the dominant component of plant biomass. The following summer, despite an increase in the mass of flower stems the relative reproductive allocation to seed formation had declined. In the final summer both the absolute weight and the relative allocation of biomass invested in sexual structures also fell. Nonstructural carbon was stored primarily in the form of fructan, which was principally located in rhizomes and roots. Massive quantities of fructan accumulated in these tissues during autumn and winter in 1988 and throughout 1989. The maintenance of rhizome weight and the fructan pool between July and August 1988, and the recommencement of rhizome expansion the subsequent spring, appeared to be fuelled by root rather than rhizome-held reserves. These results are discussed in terms of a changing emphasis in ecological strategy coincident with the shift from a disturbed to a highly stable habitat. The implications of these changes for the control of yarrow are commented upon.

Introduction

Achillea millefolium L. (yarrow) was highly valued as a palatable sheep feed on the steeper drier areas of the South Island of New Zealand but was quickly recognised as a major weed of arable land (1). Dispersal through arable land occurred through the sowing of seed contaminated by yarrow seed and fragmentation of the extensive brittle rhizome system during cultivation (3). Selective control of yarrow in arable and horticultural land by herbicides remains difficult to achieve and the cost of manual removal or repeated cultivations, aimed at depleting rhizome-held organic reserves, is high (3). This paper reports on research into the growth and carbon economy of *A. millefolium*, to develop a greater understanding of the functioning of the plant, particularly the role of the rhizome, and how more effective control may be achieved.

Materials and method

The experiment was carried out on yarrow plants, established from clonal rhizome material, and grown in containers on a field site at Lincoln University from October 1987 to January 1990. Over the first year (December 1987-January 1989) 12 replicates were harvested on each of 12 occasions at approximately

monthly intervals. Harvested plants were washed and separated into total leaves plus petioles, aerial stems, rhizomes and roots, which were then dried and weighed. During the second year the population was sampled on six dates and the replicate number reduced to six. Subsamples of tissues were analysed for fructan content.

Results

During the first summer and early autumn (December 1987–March 1988) yarrow produced mainly aerial growth. In January 1988 flower stems accounted for 42% of plant DW and rhizomes only 10% (fig 1a). Leaf and stem weight fell after March 1988 with the onset of cauline leaf and stem senescence and reached a minimum of around 20 g in early spring (September). During the subsequent growing season the production of new leaves began in October and renewed rhizome expansion began in October–November, but stem growth did not recommence until summer, between November and January. Unlike other organs rhizome biomass did not decline during the cool season and falling stem and leaf weight over autumn was largely off-set by continued rhizome growth between March and May. From July onwards rhizomes contained the greatest proportion of plant biomass and in the following summer accounted for 37% of total DW.

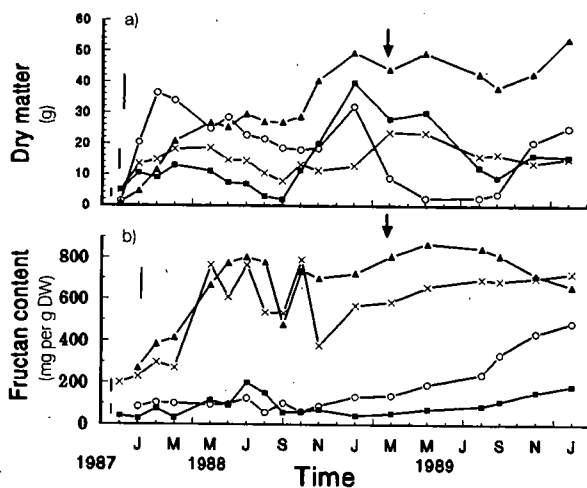


Figure 1. Dry matter and fructan accumulation in yarrow regenerating from rhizome fragments (1987-1990)
 —●— Leaf -○- Stem ▲— Rhizome x—x Root
 ▾ Live plant portions only, | 'roving' LSD of all means

In the second year (March 1989–January 1990) despite the greater age of the plants and the separation of living from of dead material, DW data confirmed the general seasonal pattern of allocation observed during the 1987/89 year (fig 1a). During this second year rhizome weight was the single largest component of plant DW contributing between 42–60%. The DW of rhizomes in 1989 was similar to the peak rhizome weights recorded the previous year. In January 1990 stem, rhizome and root weights were the same as those observed the previous January.

Yarrow accumulated non-structural carbohydrate principally in the form of fructan which reached very high concentrations in both rhizomes and roots (fig 1b). In the juvenile plants these reserves accounted for around 20% of rhizome and root DW. During the period of rapid flower stem extension from January to March 1988 fructan levels in rhizomes increased from 270 to around 400 mgg⁻¹. Fructan reserves in rhizomes and roots rose much more rapidly after flower stem growth had ceased. In late winter root-held fructan levels declined sharply from around 750 to 550 mgg⁻¹ and leaf reserves also began to fall. Rhizome fructan pools were unchanged until early spring, just prior to recommencement of growth, when leaf and total plant DW was minimal. Rapid leaf expansion occurred after September and was accompanied

by refilling of subterranean fructan pools. The recommencement of active rhizome expansion after October coincided with a sharp decline in root fructan concentration from around 800 to 500 mgg^{-1} . Fructan pools in the rhizomes were correspondingly unaffected and remained at around 700 mgg^{-1} . During the second year the massive subterranean pools were largely conserved and fructan concentrations fluctuated little.

Discussion

Achillea millefolium possesses a reproductive strategy intermediate between plants adapted to exploit conditions of low disturbance and low stress (competitors) and those adapted to low stress and high disturbance (ruderal). Competitive ruderal species such as yarrow occur in fertile habitats in which domination of the habitat by competitive species is prevented by intermittent disturbance (5). According to this model habitat stability in fertile sites favours vegetative reproduction and competitive species. In the absence of disturbance and resource limitation over an extended period, the shift in reproductive allocation from a high investment in seed production (a more ruderal habit) to a greater reliance on vegetative propagules and a more competitive strategy would be expected. When regenerating from rhizome fragments, or in all likelihood from seeds, during the summer the reproductive emphasis of immature yarrow plants is on producing new genets that may invade new habitats. Regular disturbance resulting in the fragmentation of rhizomes is likely to maintain *A. millefolium* plants in this ruderal phase of growth since competitive strategists are not adapted to regularly disturbed habitats. The reproductive emphasis in established yarrow plants is therefore on consolidating the hold of a single genet, successful in that habitat, and exploiting the area by vegetative expansion and the proliferation of genetically identical ramets.

Seasonal and ontogenic fluctuations in DW and DW partitioning were accompanied by changes in carbohydrate accumulation. Fructan concentration in rhizomes and roots was lowest in the tissues of immature plants when photosynthate was primary directed into flower stem growth. In established individuals assimilate located in other organs appears to be utilised before rhizome pools were depleted. The carbon economy of individual yarrow plants is typified by prolonged vegetative growth in autumn maintaining an active sink for photoassimilate, winter-greenness, massive accumulation of carbohydrate pools in rhizomes and roots during periods when the mass of photosynthetic tissue is greatly reduced and solar radiation and temperature conditions are unfavourable to photosynthesis. Utilisation of winter accumulated reserves to fuel regrowth in the subsequent spring with assimilate preferentially withdrawn from roots and leaf tissues while rhizome pools are maintained at high levels for most of the year. This conservation of rhizome carbohydrate pools may be important in maintaining the regenerative potential of rhizome buds.

The vegetative reproductive effort of *A. millefolium* in container grown plants, was very high in comparison with other perennial species that have been studied (2). The extensive rhizome system produced by yarrow possesses large numbers of rhizome buds (3). Each bud or single node rhizome fragment

of yarrow is able to grow and successfully regenerate into a new plant. Buds on these single node fragments showed growth activity throughout the year and lack the pronounced seasonal reproductive dormancy observed in other rhizomatous species (3). Buds on *A. millefolium* rhizomes are therefore theoretically capable of regenerating into new yarrow plants at any time of the year. When regenerating from rhizome fragments, however, yarrow plants do not achieve photosynthetic independence until about the 4-5 leaf stage, and until they do, they are entirely reliant on the nutrient reserves stored in the rhizomes (4). To successfully regenerate into new plants during the autumn and winter the potentially viable rhizome fragments require sufficient reserves of nutrients in the rhizomes. In the present study massive quantities of available carbohydrate reserves were detected in the rhizomes of mature plants over the two year study period. The reproductive potential of *A. millefolium* is therefore likely to be high at all but the most initial pre-flowering, pre-seeding stages of development. In mature plants a high reproductive potential is maintained throughout the year.

Assuming that successful regeneration from rhizome fragments depends on fructan reserves, the reproductive potential of yarrow is lowest during the early phase of regrowth following fragmentation of the rhizome system. During this phase of growth photosynthate is primarily diverted into regrowth and flower stem production and rhizome DW and fructan content are low. To be effective control strategies for yarrow require a combination of measures and should include the use of herbicide applications and /or smothering crops (3) within one to two months of cultivation.

References

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