

SHORT COMMUNICATION

BIOMASS ALLOCATION IN SUBANTARCTIC ISLAND MEGAHERBS, *PLEUROPHYLLUM SPECIOSUM* (ASTERACEAE) AND *ANISOTOME LATIFOLIA* (APIACEAE)

Summary: We analysed biomass allocation of *Pleurophyllum speciosum* (Asteraceae) and *Anisotome latifolia* (Apiaceae) to explore the ‘megaherb’ phenomenon, the apparent importance of large-leaved, colourful forbs on southern oceanic offshore islands. The two species had similar shoot dry weights, with high leaf:stem ratios. Even within the megaherb form there are differences in shoot allocations, with *Pleurophyllum* investing more biomass in rhizome than foliage, compared with *Anisotome*. The megaherb form might be attributable to responses to the physical environment, involving the pre-emption of resources such as light, nutrients, water, or space; alternatively it may be related to the paucity of woody species at this latitude.

Keywords: Megaherb; subantarctic; Southern Ocean; island; allocation; phenology; strategy; leaf:stem ratio.

Introduction

Situated in the Southern Ocean south of New Zealand between 47°40' and 52°38'S latitude are a small and scattered group of volcanic and sedimentary islands, the current representatives of subantarctic landmasses present at these latitudes possibly since the end of the Miocene (Marshall and Browne, 1909). Their flora contains several so-called ‘megaherb’ species, members of the genera *Pleurophyllum* (Asteraceae), *Anisotome* (Apiaceae), *Bulbinella* (Liliaceae) and *Stilbocarpa* (Araliaceae). These herbaceous perennial forbs have large growth forms (often more than 1 metre high or wide), with large leaves and very colourful floral displays (Hooker, 1844). Their striking growth form (Fig. 1) appears extraordinary compared with other herbaceous perennials, and may be an adaptation to their southern oceanic island environment. Six randomly chosen plants each of *Pleurophyllum speciosum* and *Anisotome latifolia* from Campbell Island were destructively harvested and resource allocations studied. These species were then compared with other herbaceous perennials to identify biomass allocation patterns that might be characteristic of megaherbs.

Methods

Campbell Island lies 700 km south of Bluff, New Zealand at 52°33'S, 169°09'E. It is an 11 000 ha windswept island with moderate rainfall (mean of 1361 mm yr⁻¹ distributed throughout the year) and

low annual sunshine hours (659). Its oceanic climate results in a mean monthly maximum temperature for the warmest month of 15.9 C and minimum for the coldest month of -2.7 C (NZ Meteorological Service, 1983).

Pleurophyllum speciosum (Hook. f.) is a rosette herb (up to 50 cm high and 100 cm wide) with large (up to 75 cm or more wide), corrugated leaves. A single plant may produce up to 16 scapes containing 10 or more capitula with pink florets, which are pollinated by insects and possibly also wind (*pers. obs.*). While considered to be evergreen, the plant reduces in size over winter, with the outer leaves dying off, and spring regrowth is possibly supported by the large rhizome. *Anisotome latifolia* (Hook. f.) is a taller (70 cm), evergreen plant with long petioles supporting the pinnate laminae; one crown produces usually one dioecious scape. The habitat of these megaherbs varies from high altitude turf-meadow to maritime megaherb-tussock grassland (Meurk, Foggo and Wilson, 1994b).

The sampled habitat of *Anisotome* and *Pleurophyllum* was an open subalpine environment comprising tussocks (*Chionochloa* and *Poa*) and occasional shrubs of *Dracophyllum*, *Coprosma*, *Myrsine* and *Polystichum* (bordering ‘*Poa litorosa* meadow and *Chionochloa*’, and ‘Tundra mosaic’ as mapped by Meurk and Given (1990)). The site was at approximately 52° 33'S and 169° 09'E at approximately 140 m above sea level.

Six randomly chosen plants (with consideration to extraction logistics) of both species were excavated and destructively harvested in early February 1997.



a)



b)

Figure 1: (a) A group of *Pleurophyllum speciosum*; (b) a lone *Anisotome latifolia*.

Roots proved difficult to harvest and were omitted from further analysis. Harvest of the megaherbs was after peak flowering time; the flowers had begun to dehisce in *Pleurophyllum* and the male scapes of *Anisotome* were beginning to rot; consequently some scape material could not be collected. The plants were sorted into foliage, reproductive matter (scapes and capitula), rhizome, and stem, and weighed fresh. They were then laid out to air-dry prior to transportation back to New Zealand.

The lamina:petiole ratio depicts allocations within the leaf to dedicated supporting vs. light harvesting tissue. While the lamina-petiole boundary is clear in *Anisotome latifolia*, the petiole in *Pleurophyllum speciosum* was arbitrarily defined as the basal part of the leaf below the expanded blade, which is considerably paler and more hairy than the lamina. In New Zealand each leaf of each plant was subdivided into lamina and petiole; reproductive material was divided into scapes, pedicels and capitula. All material was then dried for 72 hours at

65 C in a vacuum oven (-15atm.) and weighed. The quantity of tissue missing due to other sampling was visually assessed at time of weighing and values for the weighed portions adjusted.

Statistical analysis of tissue weights and allocations was by Analysis of variance (d.f. = 10) using SYSTAT (SYSTAT, 1992). Differences in allocations between large (assumed to be older) and small (assumed to be younger) leaves were examined by ranking leaves by size, with each plant standardised over the range 0 - 1. For mean lamina:petiole ratio, leaves of each plant were first grouped into quartiles by biomass.

Results

Pleurophyllum and *Anisotome* had contrasting fresh:dry weight ratios (*Pleurophyllum*: mean \pm S.E. = 10.13 ± 0.43 , *Anisotome*: 5.75 ± 0.66), indicating that *Pleurophyllum* is more succulent.

Table 1: Mean tissue allocations (% of shoot dry mass), and leaf:stem and lamina:petiole mean ratios \pm standard errors. Root material is omitted because of harvest difficulties, but subterranean rhizomes were excavated. Reproductive tissues include scapes and pedicels.

Species	Proportion of shoot dry mass (%)				Dry mass ratio	
	Stem	Rhizome	Leaf	Reproductive	Leaf:stem	Lamina:petiole
<i>Pleurophyllum speciosum</i>	1	20	52	27	61.55 \pm 9.29	5.45 \pm 0.50
<i>Anisotome latifolia</i>	2	8	81	9	61.19 \pm 10.42	1.80 \pm 0.18

The two species of megaherb did not differ significantly in their total shoot dry weights (rhizome, stem, reproductive and foliage tissue), being 220 g per plant for *Pleurophyllum* and 180 g for *Anisotome* ($P = 0.18$, Error M.S. = 2287.7). There is very little variation in dry weight between the individual plants measured (*Pleurophyllum*: S.E. = 16.69; *Anisotome*: S.E. = 21.99).

Reproductive tissue (including scape) in *Pleurophyllum* makes up three times the proportion of shoot compared with *Anisotome* (Table 1). *Anisotome* is dioecious, and as collection occurred late in the summer when male flowers were dying off not all reproductive material was sampled. The single female plant has a notably higher allocation to reproductive biomass (20%) compared with an average of 6% for the male plants.

Allocations to the non-reproductive shoot are comparable between the two species (mean \pm S.E. for *Pleurophyllum* = 162g \pm 15.96, and 163g \pm 7.93 for *Anisotome*; $P = 0.9$, Error M.S. = 1728.9), though *Pleurophyllum* has a higher allocation to rhizome ($P = 0.001$, Error M.S. = 17.45), and *Anisotome* invests a high percentage of resources in foliage (Table 1; $P = 0.000$, Error M.S. = 43.85).

Pleurophyllum has similar leaf numbers to *Anisotome* (mean \pm S.E. = 17.0 \pm 1.5 and 20.5 \pm 2.7 respectively, $P = 0.2$, Error M.S. = 28.65). There is a higher proportion of leaves in the lowest biomass class in *Pleurophyllum* compared with *Anisotome*, though the rest of the range of leaf sizes is similar (Fig. 2). A difference in leaf size patterns between the two species is suggested (Kolmogorov-Smirnov, using the combined data for all plants: $P = 0.07$).

Both species have similar leaf:stem biomass ratios (Table 1; $P = 0.98$, Error M.S. = 585.19). *Pleurophyllum* has a mean lamina:petiole ratio of 5.45, three times the ratio for *Anisotome*. In *Anisotome* the laminae of the smallest quartile of leaves contribute a large proportion of the leaf (Fig. 3; $P < 0.001$, Error d.f. = 38, Error M.S. = 1.58). This trend changes during foliage development with the largest leaves placing proportionately more resources into petioles. In *Pleurophyllum* these ratios have a reverse trend, with the laminae dominating the allocations of the largest leaves.

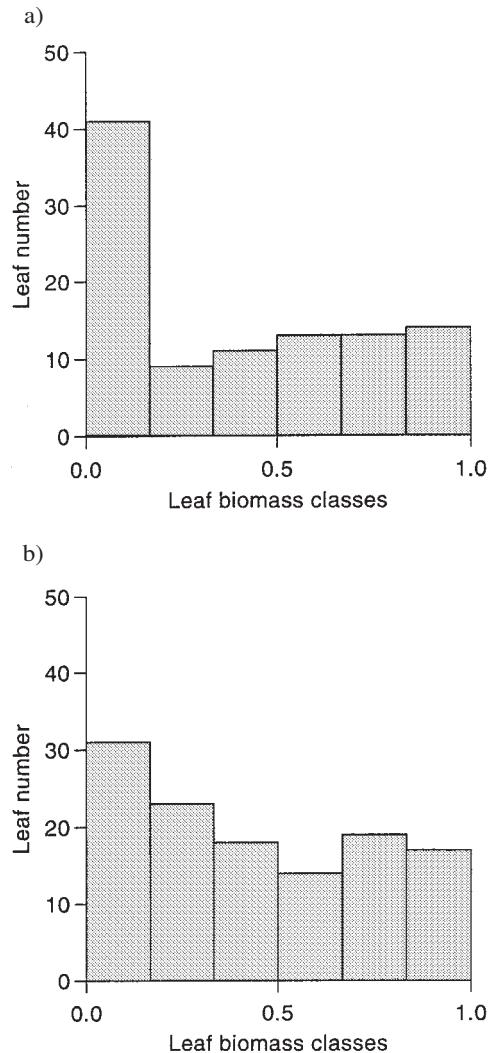


Figure 2: Frequency distribution of leaf biomass in six classes for (a) *Pleurophyllum* and (b) *Anisotome*, standardised per plant from 0 - 1, and totalled over six plants of each species.

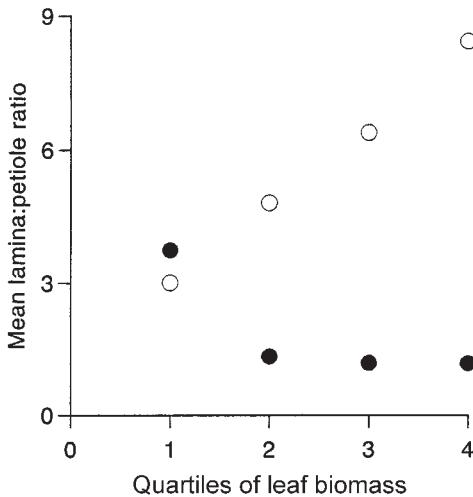


Figure 3: Mean lamina:petiole ratios for each quartile of leaves when leaves are ranked by biomass from smallest (1) to largest (4) for *Pleurophyllum* (○) and *Anisotome* (●).

Discussion

Herbaceous species with large leaves are a conspicuous feature of the vegetation on southern oceanic islands and have long been commented upon by botanists and naturalists (e.g., Hooker, 1844, Cockayne, 1903, Meurk *et al.*, 1994b). Do these species really have unique features that set them apart from other herbaceous species?

Strategies of *Anisotome* and *Pleurophyllum*

The two megaherb species studied have very similar standing crops at the time of harvest (early February, i.e., late summer). They show a higher leaf:stem ratio (61.2 for *Anisotome* and 61.5 for *Pleurophyllum*) relative to other herbaceous plants (2.5 ± 1.65 , $n = 10$; Hickman, 1975; Hickman and Pitelka, 1975; Bostock and Benton, 1979; Abrahamson and Caswell, 1982; Gross, 1983; Jolls, 1984). Allocations to laminae within the leaf show considerable variation between the two species, with the petiole being small in the rosette of *Pleurophyllum*, and an important component of biomass in *Anisotome*.

Rhizome storage of carbohydrates is a key factor in maintenance and possible support of vegetative expansion, at least in alpiners (Mooney and Billings, 1960; *c.f.* Hadley and Rosen, 1974). The shoot allocation (excluding reproductive biomass) to rhizome in *Anisotome* is considerably lower than in *Pleurophyllum*. *Anisotome* overwinters

at a size comparable with the summer form (with "retained vegetative tissues" - Pugliese and Kozlowski, 1990), so that this species 'exerts much influence on the winter physiognomy of the meadow' (Cockayne, 1903). *Pleurophyllum* sheds its outer leaves and stays in "perpetual somatic youth" (Pugliese and Kozlowski, 1990), reducing from around 75 cm over summer to a winter rosette approximately 25 cm in diameter (Cockayne, 1903). *Pleurophyllum* may then require a rhizome-stored energy supply to support its initial regrowth in the spring. Thus the strategies of the two megaherbs do vary substantively.

A characteristic and competitively successful strategy of tall herbs in open grasslands is rapid vegetative growth during the growing season, often resulting in a large above-ground mass (Al-Mufti *et al.*, 1977); many of the leaves will be formed during that growing season (Yoshie, 1995). *Pleurophyllum* and particularly *Anisotome* may have such a competitive strategy with leaf size distribution, and thus possibly time of initiation, apparently being continuous throughout the growing season. This suggests that any winter cessation of leaf production may be controlled by temperature, rather than intrinsically, with growth of new foliage possibly being responsive at any time of the year to warmer than usual temperatures. In comparison, phenology is more rigidly controlled by the seasons in alpine areas (Mark, 1970), which are more constrained climatically, with shorter growing seasons and more extreme temperatures. The herbaceous form typical of mainland alpine regions is still adaptive in the less extreme southern oceanic island environments.

No autumn flower bud initiation was observed here. This is unlike some New Zealand alpine plants where floral initials are set during the previous growing season and sometimes even at the beginning of the season (Mark, 1970).

Evolution of the megaherb form

Large-leaved forbs are not rare. The mainland of New Zealand has a large orbicular-leaved buttercup, *Ranunculus lyallii* (Hook. f.), leaf diameter up to 30 cm, and an apiad, *Anisotome lyallii* (Hook. f.) with leaf length up to 60 cm (Allan, 1961). *Myosotidium hortensia* (Decne), a large forget-me-not, is endemic to the Chatham Islands (off New Zealand). The Chilean *Gunnera* (lamina diameter 100 cm with a petiole often over 150 cm long), Hawaiian silversword, *Argyroxiphium* (Goldstein and Meinzer, 1983), and Kenyan *Dendrosenecio* and *Lobelia* (Schulze *et al.*, 1985; Fetene *et al.*, 1998) are other examples. Yet the syndrome of the southern islands appears different with corrugated, stereom tissue,

hairy and occasionally coriaceous laminae, a rosette form, fleshy root system, and colourful flowers.

Pleurophyllum is endemic to these southern ocean islands, while one species of *Stilbocarpa* extends to southern South Island, New Zealand. These genera contain only macrophyllous forbs. The other putative megaherb species have congeners throughout New Zealand; yet the megaphylls appear to be outside the normal size range of their genera.

While it is possible that the megaherb phenomena might be a chance evolutionary occurrence, megaphylls may convey several possible selective advantages in these subantarctic environments. Nutrient availability could be limiting as it varies with moisture holding capacity and acidity of peat, the main growing medium on the island (Meurk and Foggo, 1988). Large leaves may intercept nutrients from marine aerosols (Meurk *et al.*, 1994a), channelling resources directly to the stem base and onto roots (Enright, 1987; Agnew *et al.*, 1993). Alternatively, Wardle (1991) has suggested that a "greenhouse space" is set up between the large overlapping leaves of *Pleurophyllum*, with leaves acting as solar panels and focussing radiation towards the growing apex. Such temperature increases are as much as 25°C above ambient air in the Hawaiian montane silverswords, *Argyroxiphium* (Melcher *et al.*, 1994). Detrimental effects of cold are further reduced by decreases in wind speed and accompanying reductions in transpiration losses that are associated with the rosette growth form (Regehr and Bazzaz, 1976). Light is also often the limiting resource in open sites with tall herbaceous vegetation (Yoshie, 1995). In *Anisotome* the high allocation to petiole projects the leaves above the surrounding herb canopy, conferring a competitive advantage. By contrast, rosettes, such as *Pleurophyllum*, may suppress other competing herbs with their large rigid leaves.

The megaherb form might also be a response to the paucity of woody species. Yet the environment can sustain these as the tree daisy *Olearia lyalli* occurs on the more northerly of the islands and is invasive on the Auckland Islands (50° 45'S) (Lee *et al.*, 1991). The shrubby *Dracophyllum*, found on most subantarctic islands, including Campbell Island, tends to form thickets but mainly on the coastal fringes, while the Auckland Islands have a species of *Metrosideros*, also growing coastally. Elsewhere, megaherbs are aggressive, actively reoccupying their former habitat since the removal of exotic grazers (Meurk, 1982).

So the megaherb growth form must provide some adaptational advantages via pre-emption of resources and therefore be a derived syndrome.

Certainly floral colour (other than white) is a derived element in subantarctic *Abrotanella* (Swenson and Bremer, 1997). Other aspects of the megaherb syndrome might also have evolved *in situ*.

Conclusions

This work is the first biomass allocation study of subantarctic island megaherbs. These species invest a large proportion (50-80%) of their shoot biomass in leaf; consequently, their proportionate rhizome and stem allocation is low. Even though strategies differ within the growth form, e.g., varying allocation within the leaf to lamina and petiole, these results support the suggestion that there is a 'megaherb' phenomenon, a growth strategy different to other herbaceous perennials, enabling these species to be a dominant and characteristic feature of subantarctic vegetation.

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