REGENERATION OF SUBANTARCTIC PLANTS ON CAMPBELL ISLAND FOLLOWING EXCLUSION OF SHEEP

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SUMMARY: Permanent transects, established in 1970 to monitor the effects of sheep grazing on subantarctic palatable and dominant plants, are assessed. Sheep have a detrimental effect on most species considered, but regeneration is vigorous on the sheep-free side of a fence-line dividing Campbell Island.

INTRODUCTION

A fence was erected across the St Col Ridge of Campbell Island (Fig. 1) early in 1970, and feral sheep *(Ovis aries)* (Wilson and Orwin, 1964) were exterminated north of the line (Bell and Taylor, 1970). The aims of the fencing project were –

1. to assess the effects of sheep grazing on the native biota;
2. to remove the immediate threat to plant species and communities;
3. to help determine appropriate management policies for the Campbell Island reserve; and
4. to permit continuing study of the feral sheep (Wilson, 1979; Taylor, 1980).

The numbers of royal albatross *(Diomedea e. epomophora)* and remaining sheep have since been regularly monitored (Dilks and Wilson, 1979) and 21 permanent vegetation quadrats have been mapped at five-year intervals (Meurk, 1980). A further six quadrats were established in early 1981 to complete coverage of major vegetation types (Oliver and Sorenson, 1951; Meurk, 1977, 1980; Meurk and Given, in prep.).

In summer, 1975/76, it was apparent that dramatic vegetation changes were in progress in the *Poa litorosa* meadows and swards north of the fence. However, the mapped quadrats covered too little of that area to adequately reflect the initial stages of recovery. To overcome this, transects were defined extending the length of the fence-line in the open tussock and meadow country west of the continuous scrub (Fig. 1).

This paper records measured responses along the transects of 13 important plant species and one hybrid during the first 10 years of the experiment. Data are presented that will allow future comparisons.

METHODS

A 2 m broad transect was established along each side of the fence in summer, 1975/76. The paired transects were divided into seven straight sections, delimited by the corner posts at points where the fence-line altered course, and numbered from the western cliffs. For sampling purposes, the sections were further divided into units, each corresponding to the distances between fence posts, about 5 m apart. These sampling units are also numbered within each section, from west to east. The location and layout of the transects, topography, and vegetation are illustrated in Figure 1.

Within each sampling unit, on both southern, sheep *(S)* and northern, non-sheep (N) sides of the fence, the endemic, subantarctic megaherbs *(Anisotome* spp. *Pleurophyllum* spp., *Stilbocarpa polaris),* palatable tussock grasses *(Chionochloa antarctica, Poa foliosa, Hierochloe* spp. patches), and shrubs *(Dracophyllum* spp., *Coprosma* spp., *Myrsine divaricata)* were counted and the shrub and tussock categories measured (live height x breadth or basal diameter). These observations, first made when defining the transects in 1975/76, were repeated in summer, 1980/81.

RESULTS

Changes between 1970 and 1975/76

These have been largely inferred from differences between N and S (Table 1).

(i) Above the western cliffs (section 1) a short 0.01 m tall grazed turf (S, seasonally obscured by taller *Bulbinella rossii)* thickened to 0.1-0.15 m (N) largely owing to the growth of *Poa pratensis* (from data not in tables).

(ii) The numbers of *Anisotome latifolia,* and to

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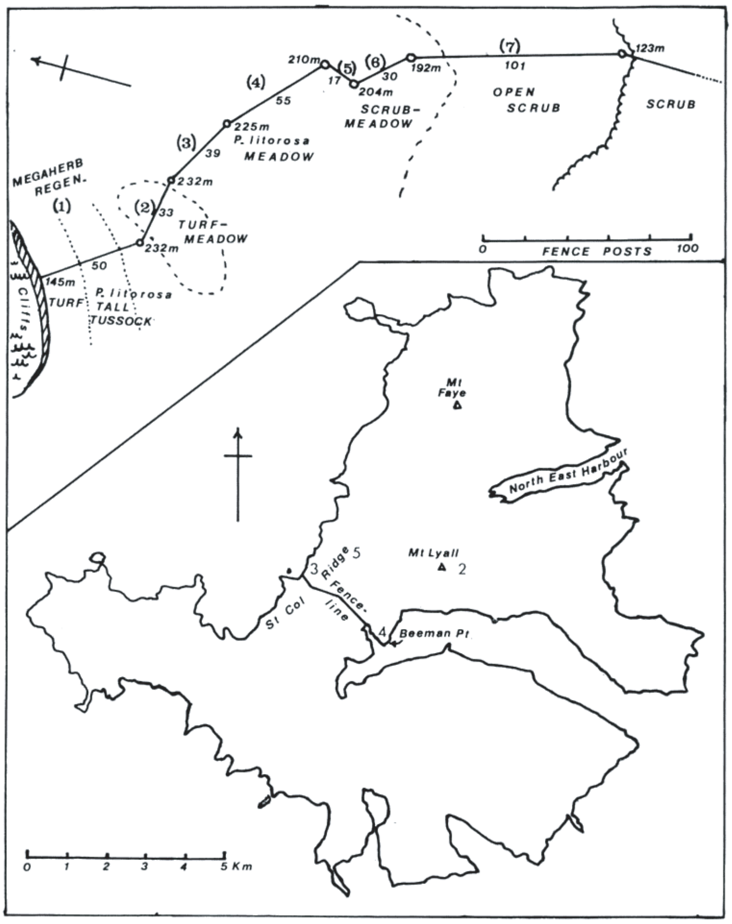

FIGURE 1. *Map of Campbell Island showing position of the dividing fence and locations of Figures 2-5. Upper inset shows detail of the double transect (scale refers to approximate ground distances in terms of average fence-post intervals). Section numbers (in brackets), altitudes at junctions of transect sections, number of sample units per section, and general vegetation features are indicated. Transect length of section (7) varies according to the purpose.*

a lesser degree *Pleurophyllum speciosum, Stilbocarpa polaris* and *Poa foliosa* (outside the transect), increased by over 100 % along the steep maritime section (N, 1*).

(iii) *Pleurophyllum hookeri* and *P. speciosum* seedlings were apparently present in the induced turf-meadow of the ridge crest (S, 2) from the outset. Numbers of *P. speciosum* plants "increased (N) whereas contrasting differences in *P. hookeri* were non-significant. However, only plants of these species no longer suppressed by grazing (N), attained flowering maturity.

(iv) *Chionochloa* tussock numbers increased by over 4000% across the induced *Poa litorosa* meadow sections (N, 2-7) of the transect.

(v) Shrub density is greater toward the east (leeward) and continuing recruitment (Zotov, 1965; Meurk, 1977, 1980) may reflect improving climates (Salinger and Gunn, 1975; Salin-

* North transect, section 1.

TABLE 1. *Numbers of plants (clones) per 100 sample units recorded in summer* 1975/76, *in each section (1-7) of the transects on the north (N) and south* (S) *sides of the fence dividing Campbell Island; total number of plants in each transect; and Chi square values, with Yates' correction, for the differences between N and* S. *Number of sample units per section are recorded in Figure 1 but sampling* in *section 7 was restricted to the 86 (herbs) and 15 (shrubs) western most sampling units only.*

Species	Transect	Plants per 100 sample units in Transect Section: 1	2	3	4	5+6	7	Total Plants Recorded	X^2 (1)
Stilbocarpa	N	2						1	
polaris	S	0						0	
Anisotome	N	18						9	
latifolia	S	0						0	10.1 (2)
Poa	N			2				1	
foliosa	S			0				0	
Pleurophyllum	N			1				1	
criniferum	S			0				0	
Hierochloe spp.	N	8	0					4	
patches	S	2	9					4	0
Pleurohllum	N	10	273	3				96	
speciosum	S	2	130	0				44	18.6
Pleurophyllum	N		103			2	1	36	
hookeri	S		142			0	0	47	1.2
Chionochloa	N	4	58	18	62	155	40	169	
antarctica	S	0	0	0	0	4	2	4	155.5
Coprosma	N	0	3	10	16	43	20	37	
cuneata	S	2	0	3	5	15	40	18	7.3
Coprosma	N	2			2	6	33	10	
ciliata	S	8			0	0	0	4	1.8
Dracophyllum	N			8	5	2		7	
hybrids	S			0	4	2		3	0.9
Dracophyllum	N			5	9	13	7	14	
longifolium	S			8	7	15	7	15	0
Dracophyllum	N		3	18	9	23	67	34	
scoparium	S		0	13	25	15	87	39	0.2
Myrsine	N			0		0	13	2	
divaricata	S			4		6	0	5	0.6

(1) Chi square ≥3.84 indicates a significant difference ($P \leq 0.05$) between plant numbers recorded in N and S transects.
(2) Value is for the four species combined.

ger, 1982) and readjustments to former vegetation destruction. *coprosma* numbers indicated a positive response to absence of browsing (N, 4-7).

Changes between 1975/76 *and 1980/81*

(i) There have been continued, generally modest, increases in the numbers of megaherbs and palatable grasses in the north and declines in the south (Table 2*). However, *Anisotome latifolia* numbers increased by more than 1000% (N). *Pleurophyllum hookeri* seedling numbers in S remained greater than in N, but the totals were dominated by 89 seedlings recorded in S, 2, sample unit 11.

(ii) Those megaherbs and tussocks, established or released from grazing during the first five years, have subsequently tended toward a population equilibrium with declining rates of numerical increase or net losses being compensated by enlargement of survivors.

(iii) Most *Pleurophyllum* plants at N, 2 were mature, up to 0.3 m across, and with leaves and inflorescences raised above the ground. Those at S, 2 were depauperate, non-flower-

* To fulfil the constraints of the percent change test (Sokal and Rohlf, 1969), 100% or no change was used as the maximum value,

TABLE 2. *Numbers of plants (clones) per 100 sample units recorded in summer 1980/81. in each section of the transects on the north* (N) *and south (S) sides of the fence dividing Campbell Island; total number of plants in each transect; percent change between 1975/76 and 1980/81; and percent comparison test statistic (ts) for difference in change between N and S. Number of sample units per section as for Table 1. Suffix s refers to numbers of, or includes seedlings.*

Species	Transect	Plants per 100 sample units in Transect Section: 1	2	3	4	5+6	7	Total Plants Recorded	% Change	t_s Value (1)
Stilbocarpa	N	2						1	0	
polaris	S	0							0	0
Anisotome	N	236	3					119	+1222	
latifolia	S	0	0					0	0	+ 9.4
Hierochloe spp.	N	16	0					8	+ 100	
patches	S	0	0					0	− 100	+4.4
Poa	N	4				3		3	+ 200	
foliosa	S	0				0		0	0	+3.1
Pleurophyllum	N	28	270	3				104	+ 8	
speciosum	S	2	39	0				14	− 68	+13.7
Pleurophyllum	N	121	230s				1	41 77s	+14 +114s	
hookeri	S		376s				0	124s	+ 164s	−c.5.7s
Chionochloa	N	6	73	33	71	158	49	195	+ 15	
antarctica	S	0	0	0	0	0	0	0	− 100	+6.2
Coprosma	N	6			24	83	140	76	+ 105	
cuneata	S	2			2	9	47	13	− 28	+5.3
Coprosma	N	4				4	27	8	− 20	
ciliata	S	2				0	13	3	— 25	0.2
Dracophyllum	N			15	4	17	20	19	+ 171	
hybrids	S			3	7	4	13	9	+ 200	
Dracophyllum	N		3	5	11	15	13	18	+ 29	+5.7 (2)
longifolium	S		0	3	7	13	0	11	− 27	
Dracophyllum	N			23	9	34	80	42	+ 24	
scoparium	S			3	15	15	87	29	− 26	
Myrsine	N				2	0	20	4	+ 100	
divaricata	S				2	2	0	2	— 60	+2.8
Pleurophyllum	N						1	1	0	
criniferum	S						0	0	0	0

(1) t_s value $\geqslant$ 1.96 indicates a significant difference (P $\leqslant$0.05) between percent changes in N and S transects. + = N > S, — = N < S.
(2) Some changes result from reinterpretation of hybrids so t_s values are for all *Dracophyllum* spp. lumped.

ing "seedlings", 0.03-0.05 m across, with leaves appressed or even recessed into the peat.

(iv) *Anisotome* and *Stilbocarpa* plants have in creased in size (N), typically from c. 0.1 m broad and tall in 1975/76, to about 0.3 m broad and 0.2m tall in 1980/81 (data not in tables).

(v) *Chionochloa* tussocks have grown (by c. 0.16 'm in height, Table 3) to about 0.2-0.5 m tall (N). This has led to the overtopping of the rather diffuse tussocks of *Poa litorosa* which had established and characterised these meadows (sections 3-6) in the early decades of this century, after the original *Chionochloa* cover was burnt and grazed out (Zotov, 1965).

(vi) The numbers of *Coprosma cuneata*. *Dracophyllum* spp., and to a lesser extent, *Myrsine divaricata* shrubs increased in N and decreased in S (Table 2).

(vii) Numerical and (non-significant) dimension increments of *Dracophyllum* and *Coprosma* species have been less in the south, suggesting an effect of browse and/or physical damage by sheep (Tables 2, 3, 4). The average annual diameter increment for all *Dracophyllum* spp. was 24.± 3 mm (n = 63), or 27 ± 3 mm excluding zero values (n = 55). The average annual height increment in *Dracophyllum*

TABLE 3. *Average 1981 heights and average increments in height (mm ± S.E.) over the period 1975/76 — 1980/81 for a sample of plants from each section (1-7) of the north (N) and south (S) transects on Campbell Island.* Chionochloa *values are for the largest tussock of each sample unit. Sample size (n) in parentheses. Data for* Dracophyllum *plants in section 7 are from 19 sample units only.*

Species		Transect	Heights and Increments (mm) for Transect Section: 1	2	3	4	5+6	7
Chionochloa antarctica	Height	N	240±20 (2)	205±21 (13)	344± 37 (10)	481±30 (17)	421±31 (22)	338±43 (6)
	Increment	N	165±95 (2)	141±19 (12)	214± 52 (10)	161±35 (16)	—	95±43 (6)
Coprosma cuneata	Height	N	255±55 (2)	—	(1975 3+4: 199±46) (11)		—	304±27 (14)
	Increment	N	26±55 (2)		Not Recorded			
Dracophyllum hybrids	Height	N			293± 53 (6)	280±60 (2)	205±41 (8)	142±20 (5)
		S			260 (1)	350±64 (4)	190±70 (2)	250±70 (2)
	Increment	N			120± 47 (5)	155±65 (2)	125±34 (8)	122±15 (5)
		S			70 (1)	43±24 (4)	15±15 (2)	1± 1 (2)
Dracophyllum longifolium	Height	N		100 (1)	300±160 (2)	405±97 (6)	341±62 (7)	125± 1 (2)
		S			390 (1)	438±41 (4)	352±39 (6)	—
	Increment	N		100 (1)	90± 50 (2)	138±29 (6)	123±20 (7)	75±45 (2)
		S			60 (1)	125±76 (4)	158±47 (6)	—
Dracophyllum scoparium	Height	N			271± 49 (9)	300±59 (5)	236±28 (16)	239±41 (17)
		S			160 (1)	308±52 (8)	250±56 (7)	208±28 (33)
	Increment	N			138± 35 (9)	40±22 (5)	119±23 (16)	117±23 (16)
		S			60 (1)	54±26 (8)	71±26 (7)	113±24 (13)

TABLE 4. *Average 1981 diameters (basal for* Chionochloa*), and average increments in diameter (mm ± S.E.) over the period 1975/76 — 1980/81 for a sample of plants from each section (1-7) of the north (N) and south (S) transects on Campbell Island. Number of plants measured (unless specified), and other details are as for Table 3.*

Species		Transect	Diameters and Increments (mm) for Transect Sections: 1	2	3	4	5+6	7
Chionochloa antarctica	B. Diam.	N	200	108±19	153± 14	228± 18	204± 15	153± 9
	Increment	N	—	—	86± 16	—	—	—
Coprosma cuneata	Diam.	N	200±50		(1975 3+4: 588±103)			
Dracophyllum hybrids	Diam.	N			288± 68	255± 95	330± 87	188±45
		S			320	313± 36	230± 60	405±95
	Increment	N			197± 48 (3)	105± 55	204± 42	130 (1)
		S			—	30± 24		—
Dracophyllum longifolium	Diam.	N		80	260±100	448±119	267± 38	75± 1
		S			220	428± 44	308± 51	—
	Increment	N		80	160 (1)	106± 29 (5)	66± 20	70 (1)
		S			—	67± 38	315±105 (2)	—
Dracophyllum scoparium	Diam.	N			297± 45	396± 97	303± 35	322±63
					270	416± 76	324± 82	325±59
	Increment	N			200± 50 (2)	66± 18	157± 36	108±22 (4)
		S			—	105± 46	135± 15 (2)	210±33 (4)

spp. was 22 ± 2 mm (n = 129) or, excluding zero values, 24 ± 2 mm (N, n = 85) and 18 ± 3 mm (S, n = 44). The difference in height increments beween N and S approaches statistical significance (t = 1.84, 0.1 > P > 0.05). Primack (1978) demonstrated a similar depression of shrub growth with grazing, but found that shrub recruitment was enhanced.

Discussion

Elsewhere in the north of Campbell Island, comparable trends to those described above are apparent. *Pleurophyllum speciosum, Anisotome antipoda* and, to a lesser extent, *Stilbocarpa polaris* and P. *hookeri* have invaded, from their former rock ledge sanctuaries, the upper alpine *Marsippospermum* rushherbfields (Fig. 2). Mature P. *hookeri* has almost blanketed the surfaces of the upper, alpine, cushionbogs (Fig. 3) and the taller P. *criniferum* now adds its majestic presence to the lowland, tall-sedge swamps (Fig. 4);

Hierochloe spp. commonly form extensive patches in grassland meadow and, in company with *Chionochloa,* are particularly noticeable along Faye Ridge. This region, being devoid of major rock outcrops to provide sanctuary for seed sources, has not yet experienced the proliferation of megaherbs observed in other sheep-free areas.

Luzula crinita heads and *Damnamenia* (= *Celmisia) vernicosa* clones appear more prominent in open herbfields or meadows north of the fence.

FIGURE 2. *Regeneration in an upper alpine tall rush herbfield, sheltered slope, near the summit of the Lyall Ridge (370 m a.s.l.). The now dominant Pleuro-*phyllum speciosum, *together with* Bulbinella rossii, *obscure the co-dominant* Marsippospermum gracile. Anisotome antipoda, *sparse* Poa litorosa *and* Pleurophyllum hookeri *are also present. (January* 1981).

FIGURE 3. *Regeneration of* Pleurophyllum hookeri *(stems* c. *0.3 m tall) on upland cushion/turf meadow, north St Col Ridge* (215 *m a.s.l.). Short tussock plants are* Poa litorosa. *North East Harbour lies below to the east. (February* 1981).

FIGURE 4. *Regeneration of* Pleurophyllum criniferum (c. *1 m tall) in lowland fen dominated by* Poa litorosa *and the largely obscured* Carex appressa, *Beeman Point* (*15 m a.s.l.).* Bulbinella rossii *is a minor dominant and on the drier slopes behind is the shrub* Dracophyllum scoparium. *(February 1981).*

Similarly *Ranunculus pinguis* now seems to be more vigorous on fellfields and screes away from the protection of crevices (N).

The superlittoral and maritime tussock megaherbfields of *Poa foliosa. Stilbocarpa polaris, Anisotome latifolia* and *Pleurophyllum speciosum,* restricted since farming to such refugia as rock bluffs, coastal cliffs and off-shore pristine stacks (Foggo and Meurk, 1981), are now undergoing reformation. This community type was naturally associated with fertile coastal sites of shallow, mineral, even calcareous,

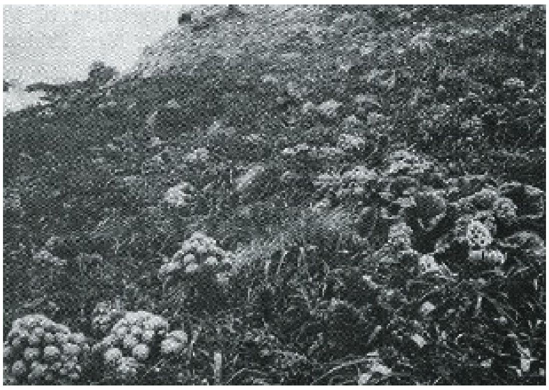

FIGURE 5. *Regenerated maritime megaherbfield, northwest St Col Ridge (120 m a.s.l.). Dominant species are* Anisotome latifolia, Bulbinella rossii *(formerly dominant over turf),* Stilbocarpa polaris, Pleurophyllum speciosum, Poa litorosa *and* Poa foliosa. *(January 1981).*

well-drained peats (Campbell, 1981), or with biotic sites, and owed its survival against the competition of taller species to its tolerance of exposure and / or marine animal disturbance. The palatability of these species subsequently meant their total demise on all accessible sites. They were replaced by native and introduced flat herbs and sward forming graminoids which, with the intrinsic fertility of the sites, remained "sweet" enough to grazing sheep to ensure perpetuation of the turfs. The prolific seeding of the megaherbs along the western cliffs continued to deluge the leeward hinterland with propagules, but only now are appropriate sites north of the fence receptive to this regenerative force. In the 10 years since sheep were removed, the swards have erupted (N) in ways dependant on the species already established and proximity to seed sources. In places, adventive grasses *(Poa pratensis, P. annua, Festuca rubra, Agrostis tenuis)* have developed a thick sole, clipped *P. litorosa* turfs (< 0.15 m) have regained their more familiar tussock form 0.5-1 m tall (cf. Taylor, 1971: Fig. 22; Dilks and Wilson, 1979: Fig. 6), and *P. foliosa* and the megaherbs have invaded with such vigour (Fig. 5), that the scene recalls colourful descriptions of pristine "Fairchild's Garden" on Adams Island (Chapman, 1891: 505).

One of the most drastic effects of the farming era (Meurk, 1977) on Campbell Island's vegetation was the virtual elimination of the *Chionochloa* tussock grassland that had formerly dominated a broad zone from about 80-330 m (Cockayne, 1903). It had seemed to me that the advantage gained by the less palatable *Poa litorosa* (and shrubs) in establishing after the disturbances would be overcome by the "climax" *Chionochloa* only after protracted competition. A belief that C. *antarctica* and P. *litorosa* had only subtly different niches was developed initially from observations in this highly modified, and therefore weakly competitive, Campbell Island setting. It is now apparent, and the distinction is obvious on the less modified Auckland Islands (Godley,]965), that *P. litorosa* is vigorous, forming the renowned subantarctic giant tussock grasslands only in maritime situations subjected to a continual rain of salt spray or where fertility is otherwise supplemented around biotic sites and swamp-flushes (see Cockayne, 1901: Fig. 1). On the other hand *Chionochloa* is now demonstrating its very considerable tolerance of, and competitive superiority on, the infertile deep acid peats of the rolling uplands. The prospect now, in the absence of grazing, is a reconstitution, in less than a century, of the pre-existing *Chionochloa* tussock grassland above the scrubline with an admixture of shrubs and megaherbs, particularly *Pleurophyllum speciosum* and on more boggy open sites, *P. hooker*i.

While regeneration is rampant in the north, vegetation condition in the south continues to deteriorate under the impact of grazing. In upland meadows *Poa litorosa* and shrubs, assumed to be protected by their low palatabilities, and on lowland cushion bogs, *Chionochloa* tussocks, historically protected from burning (therefore grazing) by their discontinuity have suffered (S) in recent years (Tables 1,2,3; Dilks and Wilson, 1979: Figs 7, 8). As previously demonstrated (Meurk, 1977: Table 2), sheep will graze *P. lito rosa* as other, more highly-favoured species are eliminated. However, the recession of less palatable species (S) may also be ascribed to increased pressure from the larger sheep population now being carried (Dilks and Wilson, 1979) in response to the more favourable climatic conditions of the past two decades (Salinger and Gunn, 1975; Norton, 1981; Salinger, 1982). Moreover this climatic change may have promoted the remarkably swift plant regeneration on the sheep-free half of Campbell Island (Meurk, 1977, 1980).

CONCLUSIONS

The rate of recovery of the subantarctic endemic flora north of the fence suggests that the greatly modified Campbell Island vegetation could, in the near future, regain much of its natural status. Seed sources and suppressed "seedlings" of palatable plant species in the south are a latent force which, if not grazed, would rapidly emulate the pattern of regeneration that has unfolded so dramatically in the north.

Serious and urgent consideration should be given to gleaning all that can be learned from the remaining feral grazing mammals. Administrators would then be better placed to weigh the merits of retaining a sheep population, more severely restricting their range, or finally removing them.

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