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Establishment of *Nothofagus solandri* var. *cliffortioides* by seeding in *Leptospermum scoparium* shrublands

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Abstract: Large areas of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest in the South Island of New Zealand have been destroyed by fire and replaced by grassland or shrubland. Mountain beech regenerates into grassland or shrubland mainly by slow spread from forest margins, though instances of long-distance spread into manuka (*Leptospermum scoparium*) shrubland have been recorded. To determine if manuka shrubland may be used to facilitate establishment, seed of mountain beech was sown under moderately dense and dense manuka canopies, at manuka stand edges, and in open grassland or moss-dominated vegetation at three sites in the Waimakiriri catchment, Canterbury. Seedling establishment after 2 years was strongly influenced by both site and position in relation to the manuka canopy. Rainfall during November of the first year (after seeding in April) was low and 0.3% emergence occurred at a site with stony soils on a steep west-facing slope. Mean emergence at the other two sites was greater (10.6% and 11.5%) and at those sites was greatest at manuka-canopy-edge positions (25–30% of seed sown). Few seedlings emerged in open grassland or moss vegetation and these mostly died. Survival of emerged seedlings after 2 years was high (45–100%) under manuka and at the stand edge. Greater establishment of beech seedlings at the edge of or under manuka stands is attributed to the provision of shade and possibly mycorrhizal inoculum by manuka. Further monitoring is required to determine ultimate seedling survival.

Keywords: canopy cover; direct seeding; leaf area index; manuka; mountain beech; seedling establishment

Introduction

Forests covered about 75% of New Zealand prior to human arrival (Newsome 1987), but since then much of the natural forest cover has been removed, largely by fire (Wardle 2002). In upland or montane areas, much of the land has been converted to grassland for grazing by sheep and cattle; however, in some more remote areas, land has become marginal for pastoral grazing. Additionally, some previously grazed land dominated by exotic pasture species has recently been lodged in the conservation estate for public use under the Crown Pastoral Land Act Land Tenure reform process. Such land is often vulnerable to invasion by exotic conifers and other woody weed species (Hunter & Douglas 1984; Ledgard 1988). In areas where the land was previously forested it may be appropriate to re-establish an indigenous forest cover for environmental benefits, such as carbon sequestration, soil and water conservation, and reduction in vulnerability to invasion by exotic woody weed species. Forest re-establishment through natural succession may be quite rapid in higher rainfall areas where seed can be dispersed from nearby remnant forest; however, in other areas succession may be much slower (Wardle 2002), and indigenous succession may be pre-empted by invasion of exotic species. In such areas intervention may be required to re-establish indigenous forest.

Mountain beech (*Nothofagus solandri* var. *cliffortioides*) is the dominant forest species in montane zones of the South Island east of the Southern Alps and is often the only tall forest species present (Wardle 1984). Large areas of forest in this region have been destroyed by fire and replaced by grassland or shrubland (Molloy 1969; Wardle 1984). In common with other

beeches, mountain beech regenerates mainly by slow spread from forest margins, though there are instances of long-distance spread into mānuka (Leptospermum scoparium) shrubland (Burrows & Lord 1993). Beech may share ectomycorrhizal fungi with Leptospermum, which would facilitate establishment of beech seedlings amongst mānuka (Baylis 1980; Wardle 1980; Burrows & Lord 1993). The inability of mountain beech to spread rapidly and recolonise grassland environments it once occupied contrasts markedly with the rapid spread of exotic conifer species (Hunter & Douglas 1984; Ledgard 1988), and intervention will be required to ensure recolonisation of mountain beech into areas now covered by grassland. As beech may invade mānuka shrubland, and as mānuka readily invades open, lightly grazed pasture when a seed source is available (Grant 1967), a possible strategy to accelerate beech recolonisation may be to seed beech into mānuka shrublands that have invaded grassland naturally, or that have in turn been established by seeding (Weijtmans et al. 2007).

Indigenous reforestation in New Zealand has normally been undertaken at a small scale by planting of nursery-raised seedlings, but this method is costly over large areas (Bergin & Gea 2007; Douglas et al. 2007; Davis et al. 2009). Seeding is a potentially lower cost alternative to planting forest species, and has been tested in experiments with New Zealand indigenous forest species in recent field studies (Ledgard & Davis 2004; Stevenson & Smale 2005; Dodd & Power 2007; Ledgard et al. 2008). Although further study is required, these experiments show that it may be feasible to establish indigenous forest species in some environments by seeding. We therefore sought to determine whether beech can be successfully established by seeding in high country environments in mānuka shrubland and if there are preferred microsites for establishment. These objectives were tested by sowing beech into different microsites among mānuka shrublands at three sites in the Waimakiriri catchment, Canterbury. The microsites examined were (1) under mānuka canopies, (2) at stand edges and (3) in gaps between stands. Shading enhances germination of mountain beech seed and seedling establishment (Wardle 1970; Easterbrooke 1998) and we hypothesised that initial establishment of mountain beech seedlings would be greater in shaded positions under canopies or at stand edges than in gaps between stands.

Methods

Site characteristics

Three sites aligned along an east–west transect in the Waimakiriri catchment were selected for the study (Fig. 1). The sites were previously used to assess the establishment of two exotic conifer species, Douglas-fir (*Pseudotsuga menziesii*)



Figure 1. Map showing the location of study sites at Bealey, Cass and Avoca, the Hawdon Valley seed collection site, and Castle Hill climate station in the Waimakiriri catchment. In the mapped area indigenous forest is mainly mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest.

and Corsican pine (*Pinus nigra*), in mānuka shrubland (Davis et al. 2011). Each site has dense but discontinuous stands of mānuka present, interspersed with open grassland or, at Bealey, moss vegetation. All sites are on north-west-facing slopes ranging from 4° to 19° (Table 1). The sites increase in elevation and precipitation from east (Avoca) to west (Bealey) (Table 1). The soil at Avoca is developed in loess on a terrace site and is relatively deep, in contrast to that at Cass which is a shallow stony soil on a steep west-facing hill slope, and at Bealey, which is also shallow and stony, but on a gently sloping ridge-top. Characterisation of mānuka stand structure and leaf area index (LAI) at each site is as described in Davis et al. (2011). The stands were of similar height but stem density increased progressively with increasing elevation from 2 stems m⁻² at Avoca to 5 stems m⁻² at Bealey.

Across all sites litter was a dominant form of ground cover, ranging from 11–26% in open positions to 65–94% under dense canopies. In open positions litter was composed mostly of grass, other herbaceous species or moss; this changed to predominantly leaf and small twig litter of mānuka in the moderate- and dense-canopy positions. Grasses (mainly *Agrostis capillaris* and *Anthoxanthum odoratum*) formed the dominant living ground cover in open to moderate canopy cover positions at Avoca, mouse-ear hawkweed (*Pilosella officinarum*) was dominant in these positions at Cass, while moss and lichen were dominant in these positions at Bealey.

Seedling plot installation and seedling assessment

Seed of mountain beech was collected in March 2009 from the Hawdon Valley (Fig. 1) and sown over the top of the ground layer vegetation, litter or bare soil in April 2009 in 0.25-m² plots at four positions with respect to the mānuka canopy cover at each site, the positions being stand openings, stand edges, and moderate and dense canopy cover. Plots in stand openings were located 1-5 m from stand edges, and had a mean LAI of 0.6 (range 0.4–0.8), those at stand edges were located outside of stands, but within 0.5 m of the mānuka stem bases, and had a mean LAI of 2.2 (range 1.5-3.0). Plots at moderate- and dense-canopy positions were located within stands and had mean LAI values of 4.0 (range 3.1-4.6) and 4.8 (range 4.3–5.3) respectively. There were five replicates of each canopy cover at each site. Seed sowing and subsequent plot assessment was facilitated by placing a 0.5×0.5 m grid on the ground, divided into 0.1×0.1 m squares. The location of the grid was marked using a permanent peg in each corner. Approximately 100 seeds of mountain beech were sown into the central row of five squares in the grid (seed of Douglas-fir and Corsican pine having been previously sown in the squares on the left and right of the grid; Davis et al. 2011). The seeding rate was therefore approximately 2000 seeds m⁻². Germinating seedlings were protected from browsing animals by 0.2-m-high

Table 1. Stand site and structural characteristics. Climatic data are long-term means. Structural data are for mānuka stems (mean \pm standard error).

	Latitude (°S)	Longitude (°E)	Elevation (m)	Aspect (°)	Slope (°)	Mean annual precipitation (mm)	Mean January max. (°C)	Mean July min. (°C)	Stem density (stems m ⁻²)	Stem dbh (mm)	Stem height (m)
Avoca	43°12'02"	171°53'16"	550	336	4	900	21.8	-0.8	2.10 ± 0.40	32 ± 3.0	3.6 ± 0.12
Cass	43°02'09"	171°46'32"	760	275	19	1280	19.0	-1.5	3.25 ± 0.25	21 ± 0.3	3.6 ± 0.03
Bealey	43°01'49"	171°36'47"	820	335	4	1670	18.8	-1.5	5.05 ± 1.05	26 ± 1.6	3.4 ± 0.10

cages of wire netting (18-mm mesh) pegged to the ground.

Seedlings were counted in December 2009 to assess initial emergence, one year later (December 2010), and again at the end of the second year (June 2011). Seedling mortality and survival were defined as the number of dead and live seedlings respectively, as a percentage of total seedlings observed at the first assessment. Analysis of variance (ANOVA) was used to determine if there were significant differences between the main treatments of site and canopy cover, and their interactions. Prior to analysis, seedling counts and survival data were transformed as required to better satisfy the underlying assumptions of the ANOVA. Where significant differences occurred at P = 0.05, a Student-Newman-Keuls test was used to distinguish between significantly different treatment means. Correlation analysis was used to determine if there were relationships between seedling number and survival, and LAI. These analyses used the means of the five replicates for each site (n = 12). Very few seedlings emerged at all positions at one site (Cass) and data from this site were omitted from analysis of % mortality and % survival data, because of lack of robustness of the estimates, and from examination of relationships between LAI and seedling emergence and survival as seeding numbers at Cass were too low to allow expression of relationships with LAI.

Results

Seedling emergence at December 2009 (8 months after sowing) varied with site and canopy cover (Tables 2 & 3). Mean total numbers of seedlings (living plus dead) that emerged per plot at Avoca (11.5) and Bealey (10.6) greatly exceeded those at Cass (0.3) (c. 11.5%, 10.6% and 0.3% of seed sown, respectively). The greatest numbers of seedlings emerged per plot were 65, 37 and 2 for the three sites respectively. At both Avoca and Bealey, mean total seedling numbers at the mānuka canopy edge (29.8 and 24.6 seedlings per plot respectively) exceeded those in the open (2.4 and 4.4 seedlings per plot respectively), though the difference was only significant at Avoca (Table 3). Seedling numbers under the manuka canopy were intermediate between, and did not differ significantly from, those in the open and edge positions (Table 3). At Cass, seedling numbers were low at all positions (0–0.6 seedlings per plot), but the interaction between site and vegetation cover was not significant (P = 0.08). Of the 60 plots only two, both at Bealey, had more seedlings at the second assessment than at the first, indicating that almost all seedling emergence had occurred by mid-December of the first growing season.

Table 2. *F*-values from analysis of variance of treatment effects on seedling emergence (total living and dead seedling numbers 8 months after sowing), live seedling number 26 months after sowing, and seedling mortality. For analysis of mortality, one site (Cass) was omitted because of low seedling numbers. Mortality includes that occurring in both growing years, expressed as a proportion (%) of the total number of seedlings present at 8 months. Analyses were performed after logarithmic transformation of data.

	Seedling emergence 8 months		Live seedlings 26 months		Seedling mortality	
	d.f.	F	d.f.	F	d.f.	F
Site	F _{2,59}	37.10***	F _{2,59}	18.13***	F _{1,36}	3.91
Cover	$F_{3,59}$	8.52***	$F_{3, 59}$	11.85***	$F_{3,36}$	8.50***
Replicate	$F_{4,59}$	0.78	$F_{4, 59}$	0.79	$F_{4,36}$	0.32
Site×Cover	$F_{6, 59}$	2.06	$F_{6, 59}$	2.27	F _{3,36}	6.99**

* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001

Table 3. Number of mountain beech seedlings present in the open and at edge, moderate and dense canopy positions at three sites and three assessment dates. Values for the December 2009 assessment show total (living and dead) seedlings, other assessments show living seedlings only. Standard errors are given in parentheses. Within sites and assessment dates, values without a letter in common are significantly different (P < 0.05).

	Sampling date							
Site	Position	December 2009	December 2010	June 2011				
Avoca	Open	2.4 (0.93) b	0.6 (0.40) b	0.4 (0.40) b				
	Edge	29.8 (9.88) a	14.0 (5.05) a	13.4 (5.16) a				
	Moderate	4.8 (1.59) b	3.2 (1.53) ab	3.2 (1.53) ab				
	Dense	9.2 (3.40) b	5.2 (1.93) ab	4.4 (1.69) ab				
Cass	Open	0.6 (0.40) a	0.2 (0.20) a	0.0 (0.00) a				
	Edge	0.6 (0.40) a	0.8 (0.37) a	0.4 (0.40) a				
	Moderate	0.0 (0.00) a	0.0 (0.00) a	0.0 (0.00) a				
	Dense	0.0 (0.00) a	0.0 (0.00) a	0.0 (0.00) a				
Bealey	Open	4.4 (1.29) a	0.6 (0.40) b	0.0 (0.00) b				
2	Edge	24.6 (5.89) a	14.0 (2.97) a	12.2 (2.78) a				
	Moderate	7.0 (2.02) a	4.6 (1.72) ab	3.8 (1.68) ab				
	Dense	6.4 (4.67) a	6.6 (4.87) ab	6.6 (4.87) ab				

Seedling mortality was low (0-13%) at all sites and positions at the first assessment, except in the open at Bealey where mortality was 82%. Substantial seedling mortality occurred over the following year and the number of live seedlings present at December 2010 was reduced to about half that present at December 2009 (Table 3). A further, but much smaller decline in seedling numbers occurred during the second summer-autumn period (Table 3). Seedling mortality and hence survival of seedlings at the final assessment, 26 months after sowing, at Avoca and Bealey was strongly affected by canopy cover and the interaction between site and canopy cover (Table 2, Fig. 2). Survival in the open (7% at Avoca and 0% at Bealey) was less than where there was some canopy cover (P < 0.05). Where there was canopy cover, survival ranged from 45 to 64% at all positions except under the dense canopy at Bealey where all seedlings survived.

Site and canopy-cover effects on the number of live seedlings at the final assessment remained highly significant (Table 2), and the interaction approached significance (P = 0.053). Two years after sowing, mean live seedling numbers at Avoca and Bealey (5.3 and 5.6 seedlings per plot respectively) remained substantially greater than at Cass (0.1 seedling per plot). At Avoca and Bealey, live seedling numbers were significantly greater at the edges (13.4 and 12.2 seedlings per plot respectively) than in the open (0.4 and 0 seedlings per plot respectively) with moderate and dense canopy covers having intermediate numbers of seedlings (Table 3). Live seedling numbers remained low at Cass at all positions (Table 3).

When all sites were considered in the analysis, no relationships were evident between LAI and seedling emergence or LAI and the number of live seedlings at any assessment. When the Cass site was omitted because of its low seedling numbers, curvilinear relationships were observed between LAI and seedling emergence and LAI and seedling survival. Seedling emergence increased rapidly to a peak with LAI values in the range of 2–3, before declining rapidly at LAI values above this (Fig. 3). LAI accounted for 50% of the variance in seedling emergence and 48% of the variance in total seedling numbers at the first assessment, increasing to 63% for total seedling numbers at the second and third assessments. There was a close relationship between LAI and seedling survival, with LAI accounting for 81% of seedling survival (Fig. 4). Seedling survival increased from zero or close to zero at LAI values of less than 0.8, to 50-100% at LAI values of 1.5-5.3. The fitted relationship indicated a decline at LAI values above 4, although the measured values showed no decline.

Discussion

Successful establishment of seedlings is dependent, firstly, on germination and emergence and, secondly, on survival of emerged seedlings. Emergence and initial survival of mountain beech seedlings in this study were strongly influenced by canopy cover. Our results confirm those of previous studies indicating that partial shading promotes germination and emergence in mountain beech. Wardle (1970) found greater germination under lightly shaded conditions (provided by shade cloth) than in the open at a low-elevation site. Easterbrooke (1998) compared germination of mountain beech seed in five habitat types in unshaded or shaded (by canopy vegetation) conditions at Cass, near the present Cass study site. Shade enhanced germination in all vegetation types except in beech forest, where germination was greater in canopy gaps. Wardle (1970) observed that seedlings do not naturally extend beyond the shade influence of trees where forest adjoins open grassland, but where shade is provided by tall scrub cover, seedlings are quite common up to 200 m away. Wardle (1970) considered that the shade would provide moist conditions for longer periods than in the open and suggested that the seed requires a prolonged moist period for germination to occur.



Figure 2. Seedling survival 26 months after sowing. Seedling survival is expressed as a percentage of the total number of seedlings present at 8 months. Data for Cass are not shown because of low seedling numbers. Values without a letter in common are significantly different at P < 0.05. There were no significant differences between Avoca and Bealey sites. Bars show standard errors.



Figure 3. Relationship between leaf area index (LAI) and the number of seedlings present 8 months after sowing. Data for Cass are not shown because of low seedling numbers.



Figure 4. Relationship between leaf area index (LAI) and survival of emerged seedlings 26 months after sowing. Data for Cass are not shown because of low seedling numbers.

At Avoca and Bealey, emergence was 3–6 times greater at the mānuka-canopy-edge position than under moderate or dense canopy positions. Lower moisture availability may have played a role in the reduced emergence that occurred under the denser mānuka canopies. These positions, with higher LAI, would have reduced soil moisture because of greater interception of rainfall. Under annual rainfall of 1300–1400 mm, mānuka may intercept 30–40% of rainfall (Rowe et al. 2002). Ammer et al. (2002) found that germination of European beech (*Fagus sylvatica*) seedlings sown in Norway spruce (*Picea abies*) stands declined with increasing canopy density, an effect they attributed to reduced soil moisture.

Open, unshaded sites are clearly hostile environments for establishment of mountain beech seedlings in moisturelimited environments. In the open, away from immediate shade provided by a mānuka canopy, few emerged seedlings survived. Shading improves survival by reducing seedling water loss through transpiration and soil water loss through evaporation and has been shown to improve seedling survival in a variety of tree species including European beech (Tognetti et al. 1994), red alder (Alnus rubra) (Hawkins & McDonald 1994), Norway pine (*Pinus resinosa*) (Caldwell et al. 1995) and Douglas-fir (Khan et al. 1996). Easterbrooke (1998) found the mortality rate of transplanted mountain beech seedlings to be greater in mānuka canopy gaps, created by tying stems back to enable light to reach the ground, than in shaded situations provided by undisturbed mānuka. Shade likewise reduced mortality of transplanted seedlings in beech forest and grassland. While shade may be a critical requirement for establishment of mountain beech in moisture-limited environments, the requirement for shade will diminish as seedlings develop robust root systems.

If Leptospermum and Nothofagus share some ectomycorrhizal species (Baylis 1980; Wardle 1980; Burrows & Lord 1993), mānuka roots may have provided inoculum for development of mycorrhizae on mountain beech seedlings in the present study, which would improve seedling nutrition and water relationships, and consequently seedling survival. Such mycorrhizal development should be greater, or should occur more rapidly under mānuka or at stand edges than in the open, potentially contributing to greater survival of those seedlings than seedlings in the open. Dickie et al. (2012) have recently confirmed mycorrhizal facilitation of mountain beech seedlings by kānuka (Kunzea ericoides), a species closely related to mānuka. The dual provision of a shaded environment and mycorrhizal inoculum by kānuka or mānuka might be used to promote rehabilitation of Nothofagus forest in environments where it has been removed by past human activity (Weijtmans et al. 2007; Dickie et al. 2012).

Using the present series of plots, as well as similarly deployed plots in kānuka stands, Davis et al. (2011) found contrasting survival of Corsican pine and Douglas-fir seedlings. Corsican pine survival was greatest in the open and declined progressively as canopy cover increased, whereas Douglas-fir survival increased from the open to the edge position before declining as canopy cover increased. Mountain beech in the present study showed some similarities with Douglas-fir, except that Douglas-fir had much greater survival in the open, and mountain beech survival did not decline under a dense canopy, although the curvilinear relationship that accounted for the most variance indicated a decline in survival at high LAI. This indicates that mountain beech may be more tolerant of low light conditions than Douglas-fir. Mountain beech can persist under intact forest canopies for 20 years or more before responding rapidly to canopy disturbance (Wardle 1970, 1984).

In addition to the influence of canopy cover, emergence was strongly influenced by site, with emergence at Cass being much less than at Avoca and Bealey. Possible reasons for the poor emergence of mountain beech at Cass include seed predation and unfavourable climatic conditions. The very poor emergence at Cass (0.3 seedlings plot⁻¹) contrasts strongly with emergence of Corsican pine (35 seedlings plot⁻¹) and Douglas-fir (8 seedlings plot⁻¹) seedlings sown 3 years previously in the same plots (Davis et al. 2011), indicating that the substrate at Cass was favourable for seedling emergence of conifers. Differences in emergence between mountain beech and the conifer species at Avoca and Bealey were much reduced.

Weta (Hemideina spp.) probably consume quantities of beech seed after it falls to the ground (Wardle 1984). Small amounts (0–5% depending on habitat) of predation of fieldsown mountain beech seed at Cass, which appeared to be due to invertebrates, were observed by Easterbrooke (1998). Such levels of consumption would not account for the differences between sites in beech seedling emergence observed in the present study. Mice (*Mus musculus*) and rats (*Rattus* spp.) consume beech seed (Wardle 1984; Ruscoe et al. 2005), as do some indigenous and exotic bird species. As the plots in our study were caged, only mice would have had access to the seed. Differences in predator population density between sites seems unlikely to account for the differences in emergence of beech seedlings between sites as the plots at Cass are further from beech forest, where predator populations might build up, than at Avoca or Bealey.

Seed predation by mice cannot be discounted, but it seems more likely that poor emergence at Cass was caused by a combination of low precipitation and low soil water storage capacity. Precipitation at the University of Canterbury Cass Field Station (located 1.3 km to the west of the trial site and 200 m lower in elevation) over the 2009 spring period (August–December) amounted to 473 mm and averaged 95 mm month⁻¹. However, precipitation for November was low (17 mm) and this may have caused reduced seedling emergence at Cass. November precipitation was also low (14 mm) at Castle Hill (located 14 km west of Avoca and 170 m higher in elevation, Fig. 1), so if low November rainfall alone limited seedling emergence at Cass, it should also have limited emergence at Avoca. Low water storage capacity of the shallow stony soil at Cass, along with greater exposure to westerly winds, in combination with low November rainfall, may have contributed to low seedling emergence at Cass. Although the soil at Bealey is also shallow and stony, this site has higher rainfall than Cass, being closer to the Main Divide and at higher elevation.

Site preparation practices such as cultivation and herbicide application, to reduce competition from herbaceous vegetation, have been found to improve establishment of indigenous woody species in pasture situations in New Zealand (Stevenson & Smale 2005; Douglas et al. 2007; Ledgard et al. 2008). The present study suggests that site preparation may be unnecessary to achieve initial establishment of mountain beech seedlings among mānuka stands providing shade is present. At Avoca, beech seedlings established well at edge and in moderately shaded positions where the ground vegetation cover was mostly (60%) litter and moss with lesser amounts (40%) of grasses and herbs. At Bealey, the dominant ground cover was litter and moss vegetation at all positions. This vegetation cover is likely to have been less competitive than the pasture species in the studies noted above, which were at lower-elevation improved (by fertiliser) pasture sites.

Conclusions

In this study mānuka-stand canopies and edges provided good microsites for initial establishment of beech seedlings, in contrast to gaps between stands, where most seedlings failed to establish. Mānuka-canopy shade greatly enhanced seedling emergence. Further seedling survival near or under mānuka stands was also greatly enhanced, possibly as a result of the provision of both shade and mycorrhizal inoculum by mānuka. Seedlings failed to establish at an exposed west-facing site with a stony soil, irrespective of the presence of mānuka cover. These initial results suggest that mānuka shrublands may be used to facilitate beech establishment by seeding at sites with sufficient available moisture. Further monitoring is required to determine ultimate seedling survival before seeding recommendations can be made.

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