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Effects of watering regime on growth and competitive ability of nursery-grown Cape fynbos and forest plants

P.T. Manders and R.E. Smith
Division of Forest Science and Technology, CSIR, P.O. Box 395, Pretoria, 0001 Republic of South Africa

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Indigenous forests in the south-western Cape are restricted to sheltered habitats. Two forest species (*Cunonia capensis* L. and the pioneer *Kiggelaria africana* L.) and three fynbos species [*Protea neriifolia* R. Br., *P. nitida* Miller and *P. repens* (L.) L.] were individually cultivated under three levels of water availability to determine the influence of this factor on forest distribution. A diallel experiment with all combinations of pairs of *C. capensis, K. africana, P. neriifolia* and *P. nitida* was carried out under the same treatments to investigate competitive abilities. Growth of all species under individual cultivation improved with increased water availability. Morphological indicators of water stress (leaf size and specific leaf area) did not follow predicted patterns and diurnal measurements of conductance did not differentiate between forest and fynbos species. *C. capensis* showed high levels of mortality in the dry watering regime, but *K. africana* persisted in this treatment. The diallel experiment showed *K. africana* to be a superior competitor at all levels of water availability. *C. capensis* was an inferior competitor, especially in the dry treatment. *P. nitida* was an inferior competitor with high water availability, but watering regime had little effect on the competitive abilities of *P. neriifolia*. Forest development in xeric habitats may be precluded by the inability of forest species to establish in normal summer drought conditions. Once established under wet conditions, however, pioneer species such as *K. africana* may persist and develop.

Inheemse woude in die suid-westelike Kaap is beperk tot beskutte habitatte. Twee woudspesies (*Cunonia capensis* L. en die pionierplant *Kiggelaria africana* L.) en drie fynbosspesies [*Protea neriifolia* R. Br., *P. nitida* Miller en *P. repens* (L.) L.] is individueel gekweek onderworpe aan drie vlakke van waterbeskikbaarheid om die invloed van hierdie faktor op woudverspreiding te bepaal. 'n Diallelle eksperiment is volgens dieselfde behandeling gedoen met alle kombinasies van pare van *C. capensis, K. africana, P. neriifolia* en *P. nitida* om mededingende vermoë te ondersoek. Die groei van alle spesies wat individueel gekweek is, het verbeter met groter waterbeskikbaarheid. Die morfologiese aanwysers van waterstres (blaargrootte en spesifieke blaaroppervlakte) het nie ooreengekom met die voorspelde patrone nie en die daaglikse konduktansielesings het nie tussen woud- en fynbosspesies onderskei nie. *C. capensis* het 'n hoë mortaliteitsvlak getoon onder lae waterbeskikbaarheid, terwyl *K. africana* oorleef het onder hierdie behandeling. Die diallelle eksperiment het getoon dat *K. africana* 'n beter kompeteerder was by alle vlakke van waterbeskikbaarheid. *C. capensis* was 'n swakker kompeteerder, veral onder die droë behandeling. *P. nitida* was 'n swakker kompeteerder onder hoë waterbeskikbaarheid, maar die waterbeskikbaarheid het min uitwerking gehad op die mededingende vermoë van *P. neriifolia*. Woudontwikkeling in 'n xeriese habitat word moontlik uitgesluit as gevolg van die onvermoë van woudspesies om onder normale somerdroogte-toestande gevestig te raak. As hulle egter eers onder nat toestande gevestig is, mag pionierspesies soos *K. africana* wel oorleef en ontwikkel.

Key words: Competitive ability, forest, fynbos, soil moisture.

Introduction

Indigenous forests have a patchy distribution amongst the predominant fynbos (shrubland) vegetation in the mountains of the south-western Cape (Campbell 1985). Forests are usually restricted to sheltered habitats such as streambanks, ravines or rock screes (White 1978). Restriction to these habitats is thought to be either a consequence of protection from fire, which occurs more frequently in the more flammable fynbos (Moll *et al.* 1980), or because of the greater soil moisture availability in such habitats. Forest development does occur between fires in fynbos vegetation in less protected areas (Kruger 1984; Masson & Moll 1987), especially where soil moisture or nutrient levels are higher than normal fynbos levels (Campbell 1985).

The exclusion of forest species in more open areas is thought to result from the failure of forest species seedlings to survive seasonal water deficits (White 1978). Greater and more prolonged seasonal water deficits have been measured in a fynbos habitat than in a nearby riparian habitat, but no differences in stomatal behaviour or water use efficiency were detected between adult riparian species in the riparian habitat and adult hillslope species in the xeric habitat (Richardson & Kruger 1990). However, it is very difficult to test in the field the ability of forest species to establish in dry habitats, as established individuals of forest species growing in such habitats have survived the period of greatest vulnerability to drought. Ideally, such tests should be carried out on freshly-germinated seedlings. It is also very difficult to determine what sources of soil moisture are available to individual plants in the field, some of which may have very deep roots.

The object of this study was to determine the different responses of forest and fynbos plants to levels of soil moisture during and after the establishment phase to develop an understanding of the factors limiting the establishment of forest species in fynbos. Individual plants were cultivated in separate containers, where soil moisture could be controlled, to overcome the problems with field investigations. This excluded competitive effects and did not allow plants to evade moisture stress by developing deep root systems. *Protea neriifolia* R. Br., *P. nitida* Miller and *P. repens* (L.) L. were used as representatives of large sclerophyllous fynbos shrub species, closest in size and morphology to forest species, and *Cunonia capensis* L. and the pioneer species *Kiggelaria africana* L. were used as representatives of evergreen forest tree species. Based on community distributions, fynbos species were expected to survive and grow better than forest species in dry conditions.

Plant mass at harvesting was used as the measure of the sum of each plant's physiological activity throughout its life. However, some measures of transpiration were made to allow comparisons with earlier field studies (Richardson & Kruger 1990). A selection of variables, including specific leaf areas and root/shoot ratios, were measured to determine their potential for use in the field as measures of the water stress under which a plant has developed. Competitive abilities of *P. neriifolia, P. nitida, K. africana* and *C. capensis* were measured using a diallel experiment (Harper 1977, p.267). Fynbos species were expected to be superior competitors in dry conditions and forest species were expected to be superior competitors in wet conditions.

Methods

Plants were cultivated in black plastic nursery bags 300 mm high and 170 mm in diameter when full. The bags were filled with silt from a weir in the Jonkershoek valley. Analyses of the soil, using standard laboratory techniques, were performed by the Saasveld Forestry Research Centre, George (Table 1). The soil is not too dissimilar to soils of forest and fynbos sites near Stellenbosch (Manders 1990), and the high nitrogen and phosphorus levels, slight acidity and low aluminium levels would not discriminate against forest species.

Seeds of *P. neriifolia, P. nitida* and *P. repens* were collected from the Jonkershoek valley during March 1987. Seeds were sown in seedling trays during June and seedlings were transplanted into the bags on 29 July 1987. Seedlings of *C. capensis* and *K. africana* were collected from the field and transplanted on the same day. Ten seedlings from each species were harvested during transplantation to compare initial sizes. The experiment was carried out in a greenhouse to prevent rain from affecting the soil moisture.

One plant of each species was cultivated per bag with ten replicates of each species in each of three watering regimes: wet, medium and dry. Plants in the wet regime were watered to saturation three times a week and those in the medium and dry treatments were watered with 200 ml per bag twice and once a week, respectively. The amount given to each bag in the medium and dry treatments was increased to 500 ml during the hot, dry period of 25 January to 1 April 1988. Plant mortality was noted weekly.

All bags were weeded and pesticides were used to control herbivory by *Acraea horta* L. (subfamily Acraeinae) butterfly larvae and red spider (order Acari, family Tetranychidae), both of which affect *K. africana* in particular.

The plants were harvested in December 1988. Plants were divided into roots, stem and leaves before drying to constant mass at 70°C. Leaf area and fresh mass of twenty leaves per plant were measured to determine the specific leaf area (SLA) from the relationship: SLA = (leaf surface area, dm^2) / (leaf fresh mass, g). The relationship between leaf fresh mass and leaf area was used to determine total leaf area from the total fresh mass of the leaves on each plant.

The effects of species and watering regime on total plant mass, height, total leaf area, leaf size and specific leaf area were determined by two-way analysis of variance. Significant interactions between species and treatment were identified in all variables measured. Therefore, an overall statement for each factor would have little meaning (Sokal & Rohlf 1968, p.315). For this reason, and because confidence intervals are often more useful than significance tests for multiple comparisons (SAS Institute Inc. 1985, p.471), comparisons between species and treatments were based on 95% confidence intervals about the means. The allometric relationships between root and shoot development ($R = bS^K$, where R is the root mass, S is the shoot mass and K is the allometric constant) were determined by principal axis correlation analysis of the logarithmic relationship,

$$\log_{10}R = \log_{10}b + K\log_{10}S,$$

based on a matrix of covariance. Values of K greater than unity indicate rootiness and values less than one indicate shootiness (Hunt 1978).

Stomatal conductances and ambient relative humidity and temperature were measured with a null-balance diffusion porometer (MCS 301 null balance porometer, MC Systems, Plumstead, Cape Province) designed to take measurements on whole leaves, on all the species in the dry and wet watering regimes. The principle of the null-balance porometer was described fully by Beardsell *et al.* (1972). Measurements were repeated on two leaves in similar positions on each of two plants per species for each watering regime at hourly intervals from pre-dawn until dusk on 28 November 1988 — a clear, windless, warm day (maximum temperature 34°C). The plants in the dry watering regime had last been watered a week prior to the conductance measurements, whereas those in the wet regime had been saturated three days before the measurements. The leaf areas of the sample

Table 1 Properties of the soil used for individual and diallel cultivation of plants in plastic nursery bags under different watering regimes

Soil property	Value (S.E.)
Coarse sand (0.5 – 2.0 mm) (%)	43.5 (4.7)
Fine sand (0.053 – 0.5 mm) (%)	43.0 (4.7)
Silt and clay (<0.053 mm) (%)	15.8 (1.2)
pH (H_2O)	5.68 (0.15)
Organic carbon	4.01 (1.39)
Total nitrogen (μg/g)	1102.5 (224.3)
Bray No. 2 phosphorus (μg/g)	14.9 (2.5)
Aluminium (μg/g)	0.2 (0.2)
Potassium (μg/g)	37.0 (9.5)
Calcium (μg/g)	141.8 (9.3)
Magnesium (μg/g)	28.8 (2.0)
Sodium (μg/g)	40.0 (7.7)

leaves were determined at the end of the diurnal run. Transpiration rates (T) per unit leaf area (g/cm^2.s) were approximated from the equation:

$$T = F/L\,(p_c - p_a)$$

where F (cm^3/s) is the flow rate within the porometer, L is the leaf area (cm^2), p_c (g/cm^3) is the water vapour density in the cuvette and p_a (g/cm^3) is the water vapour density of the dry airstream entering the cuvette (2% relative humidity) (Li-Cor Products Manual 1981). Total water transpired per unit leaf area (mmol/m^2) per day was derived by summing the areas under the straight lines connecting consecutive pairs of observations.

Competitive abilities were measured in a diallel experiment (Harper 1977). Two individuals of *P. neriifolia, P. nitida, K. africana* and *C. capensis* were planted in each bag, to produce all possible pairwise combinations. The same nursery bags and soil were used as for the individual cultivations. Ten replicates of each combination were grown under wet, medium and dry watering regimes, with the same treatments, planting and harvesting times as in the individual cultivations. On harvesting, root systems were washed clean, and the plants in each bag were separated and dried to constant mass at 70°C.

Analysis of plant growth followed the method of Wilson and Keddy (1986), based on the mass accumulation of individual plants. The relative increase in plant mass (RIP) per plant of species i grown with species j was calculated as

$$\mathrm{RIP}_{ij} = (\mathrm{HDM}_{ij} - \mathrm{SDM}_i)/(\mathrm{HDM}_{ii} - \mathrm{SDM}_i),$$

where HDM_{ij} is the dry mass of the plant at harvesting, SDM_i is the mean starting dry mass of species i, and HDM_{ii} is the mean dry mass at harvesting of plants in species i when grown with a conspecific neighbour. Plants which died were not included in the growth analysis. A plant with an RIP, when grown with a plant of another species, greater or less than 1 indicates better or poorer growth, respectively, in the presence of the neighbour than with a conspecific neighbour. Differences between target scores (the mean RIP of each species grown with all species of neighbours) and neighbour scores (the mean RIP of all target species with which a particular neighbour species was grown) within each treatment were based on two-way analysis of variance. Competitive superiority is indicated by high target scores and low neighbour scores. A similar analysis was performed on the relative survival of plants in each of the combinations.

Results

Individual cultivation

Initial plant sizes varied considerably between species. The dry masses were as follows: *Protea nitida*, 100.0 mg (S.E. 34.0 mg); *Protea neriifola*, 21.6 mg (S.E. 1.3 mg); *Protea repens*, 25.8 mg (S.E. 1.4 mg); *Kiggelaria africana*, 34.9 mg (S.E. 3.1 mg); and *Cunonia capensis*, 27.0 mg (S.E. 14.0 mg). This factor was not included in analyses of the final harvest of individually cultivated plants, however, as final plant sizes were several orders of magnitude greater than the original sizes and the initial pattern of size differences disappeared quickly.

Watering regime and species, and the interactions between these factors, had significant effects on all variables in the growth analyses (Table 2). All species, except *P. nitida*, had greater biomasses in the medium watering regime than in the dry watering regime (Figure 1). In the wet watering regime, all species had greater biomass than in the dry, but not consistently greater than in the medium regime. There was no pattern of different responses between forest and fynbos species within treatments. Height growth (Figure 1) showed a very similar pattern to biomass accumulation, but identified the extreme vigour of *K. africana* in the medium regime.

Total leaf areas of all species except *P. nitida* in the dry treatment were very similar to each other and exhibited similar increases in the medium treatment (Figure 2). The

Table 2 F values of two-way analysis of variance between treatment (watering regimes) and species for variables measured in growth analyses of forest and fynbos species. All F values are significant at $P < 0.0001$

Variable	Treatment	Species	Treatment × Species
Total plant mass	154.3	41.7	20.6
Plant height	113.8	67.4	12.1
Total leaf area	117.4	39.5	12.4
Leaf size	176.6	287.8	34.2
Specific leaf area	14.6	334.1	7.8

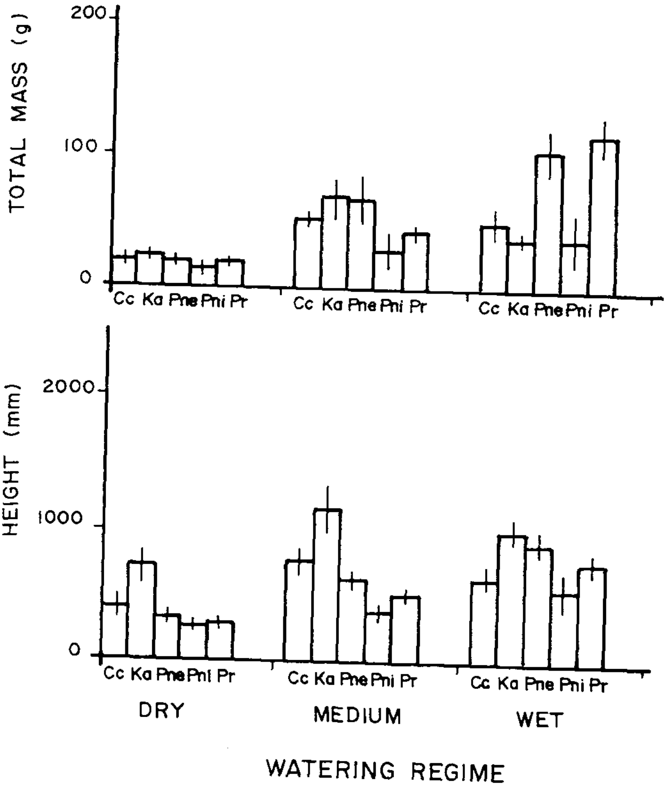

Figure 1 Total mass and height of forest and fynbos plants and an invasive alien cultivated from seedlings in July 1987 to December 1988 under three watering regimes. C.c., *Cunonia capensis*; K.a., *Kiggelaria africana*; P.ne., *Protea neriifolia*; P.ni., *Protea nitida*; and P.r., *Protea repens*. 95% confidence limits about the means are represented by vertical lines.

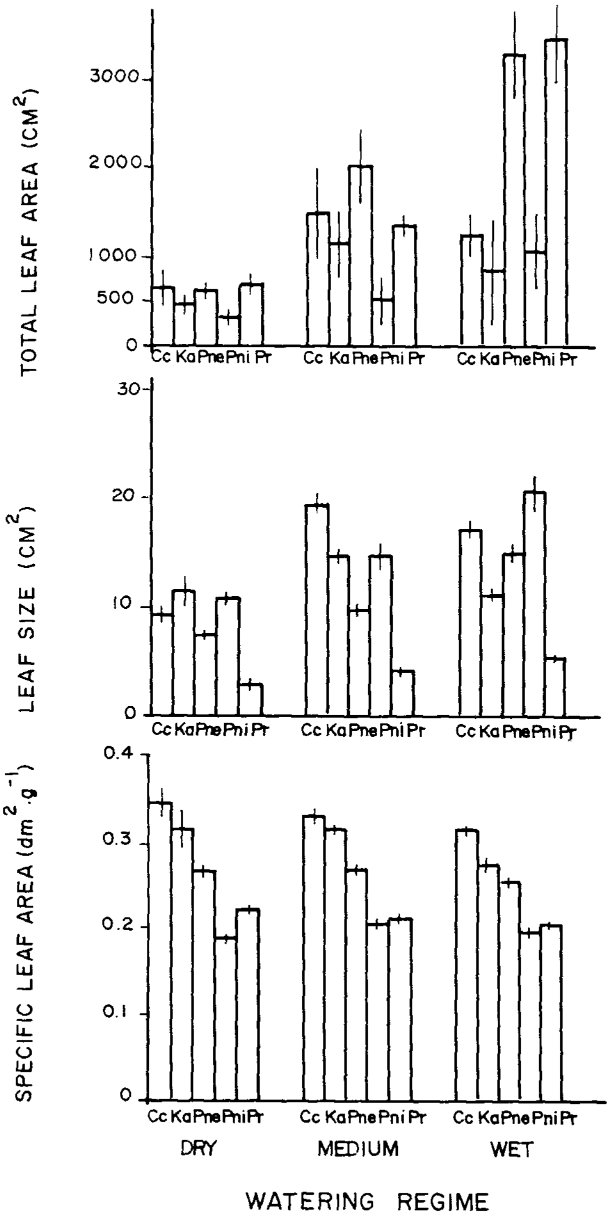

Figure 2 Total leaf area, leaf size and specific leaf area of forest and fynbos plants and an invasive alien cultivated from seedlings in July 1987 to December 1988 under three watering regimes. C.c., *Cunonia capensis*; K.a., *Kiggelaria africana*; P.ne., *Protea neriifolia*; P.ni., *Protea nitida*; and P.r., *Protea repens*. 95% confidence limits about the means are represented by vertical lines.

Table 3 Slopes (K) of principal axes describing the allometric relationship between root and shoot mass ($\log_{10}R = \log_{10}b + K\log_{10}S$) for all plants in each species and within dry, medium and wet watering regimes[a]

	Treatment			
Species	All	Dry	Medium	Wet
Cunonia capensis	1.13 (0.93)		1.04[b] (0.91)	1.01 (0.97)
Kiggelaria africana	0.72 (0.93)	0.88 (0.60)	0.74 (0.78)	0.72 (0.85)
Protea neriifolia	0.91 (0.94)	2.05 (0.92)	2.05 (0.90)	1.61 (0.93)
Protea nitida	0.96 (0.94)	1.23 (0.96)	0.70 (0.96)	0.94 (0.98)
Protea repens	0.84 (0.97)	2.99 (0.81)	3.43 (0.85)	1.52 (0.84)

[a] Figures in parentheses show the proportion of variance explained by the eigenvalue of the covariance matrix of the first principal axis. K values greater than unity indicate rootiness.

[b] Figures include plants grown under dry and medium watering regimes.

total leaf areas of fynbos species (except *P. nitida*) showed greater positive response to enhanced water availability than the forest species. Responses in individual leaf size varied between species (Figure 2). Although the sizes of *C. capensis* and *K. africana* leaves were greater in the medium treatment than in the dry treatment, there was a slight decrease in the wet treatment compared with the medium treatment. *P. neriifolia, P. nitida* and *P. repens* showed consistent increases in leaf size with enhanced water availability, but the increase in leaf size in *P. repens* was trivial compared with the massive increase in total leaf area (Figure 2), which resulted from the production of more leaves. Specific leaf areas did not vary consistently with watering regime (Figure 2). The slopes of the principal axes correlating log root mass and log shoot mass of individually cultivated forest plants did not show any clear trend (Table 3). Fynbos species, on the other hand, had greater rootiness in the dry treatment than in the wet treatment.

No plants died in the wet and medium watering regimes except for some *C. capensis* in the medium treatment. All deaths in the dry treatment occurred within the first 20 weeks of the experiment. Greatest mortality occurred within *C. capensis*. There were no mortalities in *K. africana* and very few amongst the fynbos species (Figure 3).

Stomatal conductances (median values of four leaves per species per hour) were similar for all the species in the dry watering regime. Values varied between 0 (dawn and dusk) to 80 mmol.m^{-2}.s^{-1}. Ambient temperatures ranged from 15°C at 05:00 to 34°C. Relative humidities ranged from 67 to 30%. All species responded positively to the wet regime (with the exception of *P. repens*), with conductances ranging up to 165 mmol.m^{-2}.s^{-1}. There was, however, no differentiation between conductances of forest and fynbos species. No species exhibited midday stomatal closure in either of the water regimes.

Diallel experiment

Analysis of variance showed significant effects for both target and neighbour scores, with no significant interactions, in all watering treatments (Table 4). Significant differences between target scores and between neighbour scores occurred within each treatment (Table 5). Relative competitive abilities are shown in Figure 4. Species in the upper left quadrant (high target and low neighbour scores) are superior competitors, those in the lower right quadrant (low target and high neighbour scores) are inferior competitors. *K. africana* was a superior competitor at all levels of water availability, whereas *C. capensis* was a consistently inferior competitor, but tended to greater competitive ability with increased water availability. The competitive abilities of *P. neriifolia* were little influenced by water availability. *P. nitida* was never a strong competitor, and lost competitive

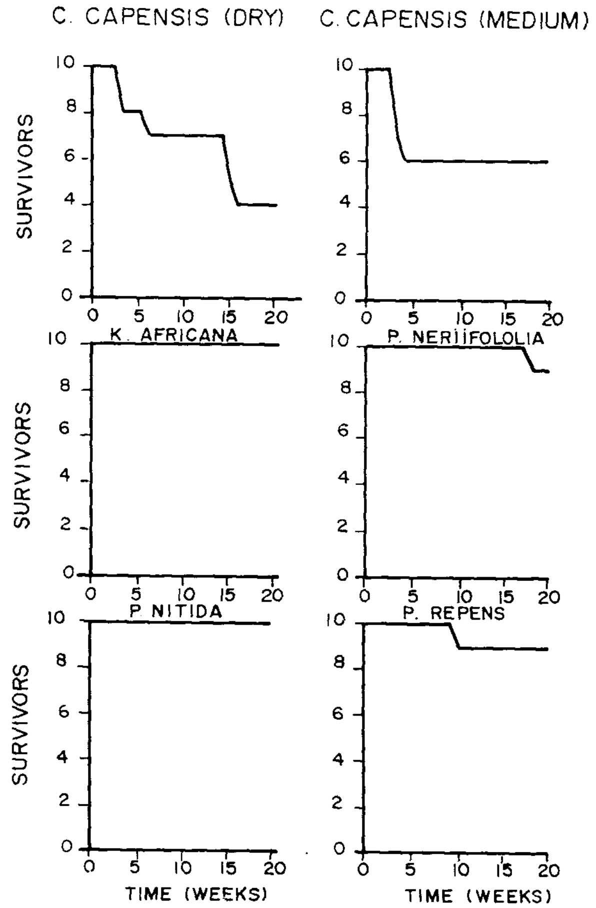

Figure 3 Numbers of individually cultivated forest and fynbos plants and an invasive alien surviving during the first 20 weeks of cultivation under a dry watering regime (see text) and numbers of *Cunonia capensis* surviving during the first 20 weeks of cultivation under a medium watering regime (see text). Cultivation began on 30 July 1987.

Table 4 Two-factor analysis of variance of the diallel competition experiment under dry, medium and wet watering regimes (see text)[a]

Source	df	ss	ms	*F*	*P*
Dry watering regime					
Factorial model	14	23.2	1.6	6.89	0.0001
Error	118	28.4	0.2		
Total	132	51.6			
Target scores	3	2.8		3.94	0.0102
Neighbour scores	3	17.3		24.03	0.0001
Interaction	8	3.0		1.58	0.1383
Medium watering regime					
Factorial model	15	25.1	1.7	6.48	0.0001
Error	160	41.3	0.3		
Total	175	66.4			
Target scores	3	13.4		17.24	0.0001
Neighbour scores	3	8.0		10.32	0.0001
Interaction	9	3.8		1.62	0.1134
Wet watering regime					
Factorial model	15	16.6	1.1	5.63	0.0001
Error	164	32.1	0.2		
Total	179	48.7			
Target scores	3	7.8		13.26	0.0001
Neighbour scores	3	7.8		13.28	0.0001
Interaction	9	1.0		0.54	0.8421

[a] Target and neighbour scores are given in Table 5.

ability as the water levels increased. No species showed evidence of mutual suppression or mutual stimulation (lower left and upper right quadrants of Figure 4, respectively).

Target survival is the survival of a species when grown with all other species, and reflects the ability of a species to persist rather than competitive ability. This variable showed very similar trends to the target score in the mass analysis (Table 6). Neighbour survival is the survival of other species in the presence of the target species, reflecting the competitive ability of the target species. This variable ranked the species differently from the neighbour scores in the mass analysis. *K. africana* in the dry treatment is associated with low survival of neighbours of other species. This identifies the species as a stronger competitor (Figure 5) than indicated by the mass analysis (Figure 4). Similarly, *P. nitida* in the dry and medium treatments, while maintaining the pattern of decreasing competitive ability with increasing water supply, is identified as a stronger competitor than shown by the mass analysis. Analysis of survival confirmed the lack of effect of water availability on *P. neriifolia* and the competitive inferiority of *C. capensis* (improving with increased water availability) indicated by analysis of mass increment.

Discussion

There is no practical method for precise control of soil moisture in numerous small containers, and the watering regimes applied in these experiments were entirely subjective. The dry regime was determined by the minimum quantity of water which appeared necessary for reasonable seedling survival, and the wet regime provided an excess of water. Although such treatments are not directly applicable to field situations, stomatal conductances for *P. repens, P. nitida* and *C. capensis* in the wet treatment were similar or greater than measured in a riparian habitat (Richardson & Kruger 1990). *P. repens* and *P. nitida* seedlings during an intensive study drought had similar conductances to those of the same species in the dry watering regime (Smith & Richardson 1990). These comparisons suggest that an objective, reasonably applicable, range of conditions existed among which comparative studies are possible.

No method was found to assess the moisture stress experienced by plants in field situations. Leaves which develop under dry conditions tend to be smaller and more divided, and have a smaller SLA (Larcher 1983). This pattern was not noted in this study and this variable has little potential for use in field studies. Fynbos species showed greater plasticity of root / shoot ratios than forest species. The *K* values greater than unity in fynbos plants in the dry treatments show a morphologically-based ability to persist during drought conditions. However, the differences between treatments are relatively minor and the values of the ratios are not very different from forest species.

Plant mortality results indicated the basis for the different establishment abilities of forest and fynbos species. Under conditions of water stress *C. capensis* is not as hardy as fynbos species. *K. africana*, however, has an ability to colonize fynbos areas (Kruger 1984), and this ability was

Table 5 Relative increases in dry mass of four plant species grown in all pairwise combinations from July 1987 to December 1988 under dry, medium and wet watering regimes (see text)*

Target species	Neighbour species				Target scores
	P.ne.	*P.ni.*	*K.a.*	*C.c.*	
Dry watering regime					
P.ne.	1.00	0.56	1.22	1.72	1.21^{a}
P.ni.	1.04	1.00	0.71	2.08	1.12^{a}
K.a.	0.92	1.31	1.00	1.91	1.24^{a}
C.c.	0.27	0.00	0.34	1.00	0.54^{b}
Neighbour scores	0.95^{b}	1.06^{b}	0.94^{b}	1.83^{a}	
Medium watering regime					
P.ne.	1.00	1.08	0.76	0.78	0.92^{b}
P.ni.	0.77	1.00	0.58	0.88	0.85^{b}
K.a.	1.65	1.55	1.00	2.02	1.44^{a}
C.c.	0.84	0.60	0.40	1.00	0.75^{b}
Neighbour scores	1.06^{a}	1.12^{a}	0.76^{b}	1.18^{a}	
Wet watering regime					
P.ne.	1.00	1.40	0.92	1.21	1.11^{ab}
P.ni.	0.56	1.00	0.41	0.71	0.72^{c}
K.a.	1.38	1.44	1.00	1.53	1.28^{a}
C.c.	0.94	1.28	0.56	1.00	0.93^{b}
Neighbour scores	0.98^{bc}	1.25^{a}	0.79^{c}	1.12^{b}	

* Target score is the mean dry mass increase of each species grown with all species of neighbours. Neighbour score is the mean dry mass increase of all target species with which a particular neighbour species was grown. Target and neighbour scores are weighted by the numbers of plants within each combination. Target and neighbour scores not significantly different from one another (Student-Newman-Keuls multiple range test, $P < 0.05$) are denoted by common superscripts. *P.ne.*, *Protea neriifolia*; *P.ni.*, *Protea nitida*; *K.a.*, *Kiggelaria africana*; *C.c.*, *Cunonia capensis*.

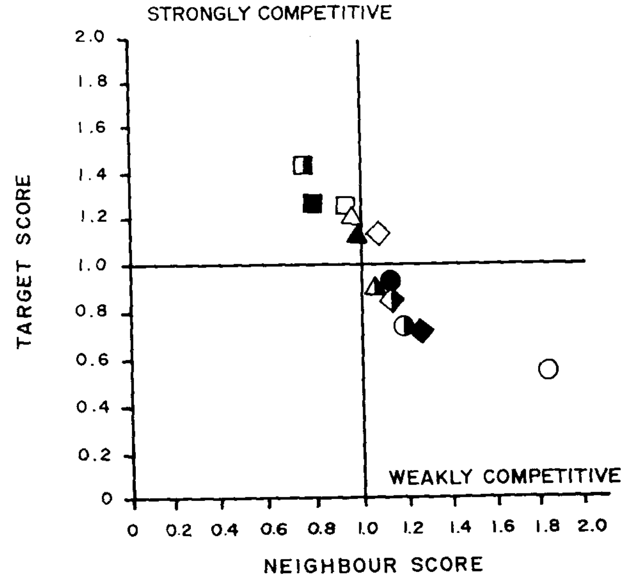

Figure 4 Relationships between target scores and neighbour scores determined by the diallel experiment. ○, *Cunonia capensis*; □, *Kiggelaria africana*; △, *Protea neriifolia*; and ◇, *Protea nitida*. Empty, half-filled and filled symbols represent dry, medium and wet treatments, respectively. Observations with high target scores and low neighbour scores represent strong competitive abilities and observations with low target scores and high neighbour scores represent low competitive abilities.

Table 6 Survival of four plant species grown in all pairwise combinations from July 1987 to December 1988 under dry, medium and wet watering regimes (see text). Numbers show survivors from the initial 10 plants of each species in each combination (20 when grown with the same species)[a]

Target species	Neighbour species				Target survival
	P.ne.	*P.ni.*	*K.a.*	*C.c.*	
Dry watering regime					
P.ne.	16	3	8	10	21
P.ni.	8	20	10	7	25
K.a.	9	10	18	10	29
C.c.	2	0	2	2	4
Neighbour survival	19	13	20	27	
Medium watering regime					
P.ne.	18	9	10	9	28
P.ni.	10	20	10	9	29
K.a.	10	10	20	10	30
C.c.	8	3	9	11	20
Neighbour survival	28	22	29	28	
Wet watering regime					
P.ne.	20	10	10	10	30
P.ni.	10	16	8	8	26
K.a.	10	10	19	10	30
C.c.	10	7	9	6	26
Neighbour survival	30	27	27	28	

[a] Target score is the total survival of each species grown with all species of neighbours excluding itself. Neighbour score is the total survival of all target species (excluding itself) with which a particular neighbour species was grown. Species abbreviations as in Table 5.

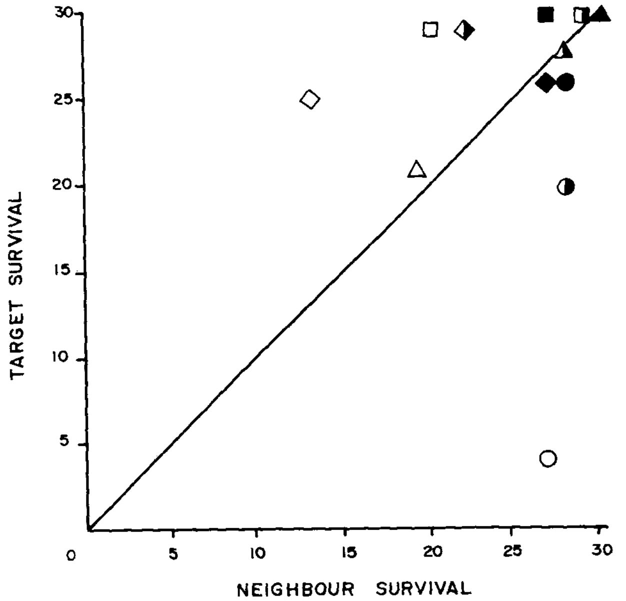

Figure 5 Relationships between target survival and neighbour survival determined by the diallel experiment. ○, *Cunonia capensis*; □, *Kiggelaria africana*; △, *Protea neriifolia*; and ◇, *Protea nitida*. Empty, half-filled and filled symbols represent dry, medium and wet treatments, respectively. Symbols above and below the line of equality represent competitive superiority and inferiority, respectively. The degree of superiority or inferiority is denoted by the perpendicular distance from the line of equality.

reflected in the survival of all plants of this species in the dry treatment.

Diurnal measurements of stomatal conductance, as in the field studies of Richardson & Kruger (1990), failed to differentiate between forest and fynbos species in any of the treatments. Such measurements, whether in the field or under experimental conditions, are made on surviving plants, i.e. on established plants. Physiological measurements are usually over relatively instantaneous time intervals, and differences during such periods may be minimal. Biomass accumulation (and survival rates in extreme cases) sum minor differences in physiological activity over the life of the plant, and provide better measures of the ability to establish and of competition.

Diallel experiments, whether involving one or several individuals of each species per container, do not include the effects of initial densities and may not reflect behaviour in multispecies mixtures. Caution is also required in the interpretation of RIP values in diallel experiments. Exploitation of a different array of resources may be reflected as apparent competitive superiority. Apparent competitive inferiority, however, may only be attributed to interspecific competition (Wilson & Keddy 1986). The low survival of neighbour species in the dry treatment in the presence of *K. africana* and *P. nitida* indicates that these species may outcompete neighbours for a resource and persist without enhanced biomass accumulation. The ability of a species to persist in certain conditions may be more important, if habitat amelioration is likely at a later stage, than its initial competitive superiority. Addition of the survival analysis to the mass analysis of the diallel experiment not only confirmed the general pattern of relative competitive abilities, but also enhanced the interpretation of the experiment.

The competitive superiority of *P. nitida* compared with *P. neriifolia* in dry conditions and the loss of this ability in wet conditions are consistent with these species' distribution ranges. *P. nitida* is associated with dry mountain ranges, whereas *P. neriifolia* is found on southern slopes of moister coastal ranges, only occurring on northern slopes in high rainfall areas (Rourke 1980). *P. neriifolia* showed little response to water availability, which is consistent with the species's tolerance of different conditions noted in the horticultural industry (Vogts 1982). Such confirmation lends credibility to other patterns demonstrated by the diallel experiment, despite the shortcomings of the design discussed above.

The restriction of forest vegetation to riparian and scree habitats is related to the enhanced water availability in these environments. Fynbos species were shown to be superior competitors in xeric habitats. Forest development in xeric habitats may well be precluded by the inability of climax forest species to establish in normal summer drought conditions. Once established, however, seedlings of forest pioneers such as *K. africana* can persist in relatively xeric environments. Therefore, given occasional establishment of forest seedlings under favourable circumstances, progressive development of forests away from typical habitats may be expected in the absence of disturbance. To some extent, fynbos species were shown to be inferior competitors in mesic environments. This may prevent invasion of mesic environments by such species and could explain the observed stability of forests in mesic habitats.

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