

## DO PLANTS EVER COMPETE FOR SPACE?

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**Abstract:** The term “competition for space” occurs often in ecological literature, but there has never been a direct demonstration of this competition. In fact it has been shown that plant canopies are mainly empty of plant organs. F.E. Clements recognized this. He suggested that one of the few situations in which competition for space would occur was in an unthinned row of radishes. Even this has never been demonstrated. We sowed radishes (*Raphanus sativa*) in a dense row and let them grow to maximum size in favourable conditions. For comparison, the same number of radish seeds were sown in a double, offset row. Squeezing the radish plants into one row was largely compensated by sideways movement of their hypocotyl/taproots, but total plant mass was reduced by 7.5%. Even this cannot be definitely attributed to competition for space. We conclude that competition for space, if it exists at all, is only a small effect even in conditions very favourable for it. It can, as Clements said, be ignored for natural communities.

**Keywords:** Clements, Competition, Radish, *Raphanus sativus*, Resource competition

### INTRODUCTION

Competition is “an interaction between individuals, brought about by a shared requirement for a resource in limited supply, leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned” (BEGON et al. 1996). But what resources can be involved? Ecologists often write of competition for physical space. This should mean that space is in limited supply and that this reduces plant growth etc. When ecologists use “space” in “competition for space” as shorthand for all resources (e.g. WILSON & HARDER 2003) discussion of competition for space may be justifiable, though it is misleading and obscures the differences between resources in their mechanisms of competition (WILSON 1988a). However, sometimes it is made clear that space is seen as a resource separate from light, water, NPK, etc., e.g. “competition is defined as ‘the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space’” (GRIME 1979, 2001) or “weeds competing for light and space in the first year of growth, rather than moisture or nutrient stress” (SAGE 1999). GRIST (1999) modelled “plant competition for light and space”. YODZIS (1986) envisaged that, “... competition for space is so different from what we normally think of as consumptive competition that it makes more sense ... to think of it as a completely different category of competition. Certainly space is quite different from any other resource”.

When such statements are made, the space concerned should be equivalent to volume, though often the assumption seems to be soil surface area, as seen clearly when the process is modelled (e.g. SILVERTOWN et al. 1992, GRIST 1999). Competition for 2-dimensional space probably does occur in some sedentary animals, for example between intertidal mussels and barnacles (CONNOLLY et al. 2001), but vascular plant communities are almost all 3-dimensional.

As far as spatial volume is concerned, CHIARUCCI et al. (2002) examined the percentage volume occupancy of eight plant communities. In spite of all the assumptions and speculation in the literature, and in spite of studies that had measured plant volume without measuring community volume such as the mensuration of foresters, the percentage occupancy had never before been measured. CHIARUCCI et al. (2002) found considerable empty space in all the communities and doubted whether competition for space occurred in plant communities. CLEMENTS (1916: 72) understood this: "In a few cases, such as occur when radish seeds are planted closely, it is possible to speak of mechanical competition or competition for room. ... However, [this] seems to have no counterpart in nature. There is no experimental proof of mechanical competition between root-stocks in the soil, and no evidence that their relation is due to anything other than competition for the usual soil factors – water, air, and nutrients". Actually, there is no evidence that it occurs between close radishes. We set out to test whether it occurred even there.

## METHODS

Seeds of radish (*Raphanus sativa* L. cv. "Yates gentle giant"<sup>1</sup>) were sown in boxes in a single dense row, seeds 1 cm apart, and allowed to grow to maximum size in favourable conditions. For comparison, the same number of radish seeds were sown at the same density per box but in double rows: two rows 2 cm apart with the seeds within each row 2 cm apart, one row staggered with respect to the other. The boxes, 20 × 20 cm, were kept out of doors, in full light, with a gap of 20 cm between boxes. They were filled with a commercial potting compost (NPK 18 : 2.2 : 11 plus minor elements). The seeds were sown on 20 January 2006. The boxes were watered as required, at least once daily, and to ensure that mineral nutrients were not limiting liquid fertiliser<sup>2</sup> (NPK 8 : 3 : 6) was added on 1 March and 1 April. The plants were harvested on 14 May 2006 at the early stages of bolting in a few of the plants. Dry weight of the leaf + stem (mainly leaf) and separately of hypocotyl + taproot (the edible "radish") was taken. There were 15 replicates in a randomized block design. As well as physical positioning, all procedures such as sowing, watering and harvesting were performed according to the randomized design.

The results were subjected to analysis of variance. In no analysis was there any appreciable or significant departure from normality, nor any heteroscedasticity. Log transformation gave no overall reduction in the slight and non-significant departures from the assumptions of analysis of variance that were present and was therefore not used (the results after transformation were essentially identical).

## RESULTS

There was 100% germination. Little mortality occurred: 1.3% in the single-row and 2.7% in the double-row boxes, not a significant difference according to Fisher's Exact Test ( $P = 0.11$ ). The lesser space available for the radish roots in the single-row treatment was

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1 Orica New Zealand Ltd.

2 "Yates Nitrosol"

Table 1. Dry mass (g) per box of *Raphanus sativa* (radish) planted in a double row or in a single row, with the significance of the difference between treatments.

Dry mass component	Double row	Single row	Reduction from double (%)	<i>P</i>
Shoot	39.61	36.59	7.64	0.2794
Hypocotyl + taproot	48.24	44.67	7.39	0.0295
Total	87.85	81.26	7.50	0.0470

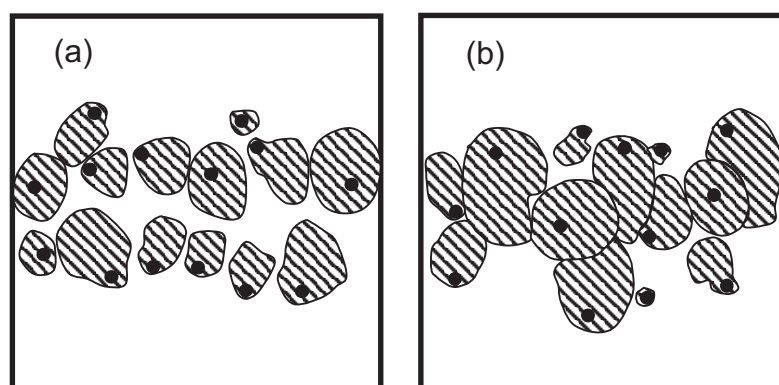


Fig. 1. The distribution of hypocotyl+taproots of *Raphanus sativa* (radish) in one replicate when sown: (a) in a single row, and (b) in a staggered row. ▨ = radish hypocotyl + taproot; ● = position of shoot attachment.

largely compensated by sideways movement of their hypocotyl/taproots (Fig. 1), but total plant mass was reduced by 7.5% (Table 1). Hypocotyl + taproot mass was reduced significantly, but not shoot mass though the effect size was similar.

## DISCUSSION

Clements concluded that there is very rarely competition for space in plant communities (CLEMENTS 1916, CLEMENTS et al. 1929). CHIARUCCI et al. (2002) measured the percentage volume occupancy of four grasslands and four shrublands (two of each in Italy and two in New Zealand) and found that above-ground space was not limiting, with only 0.44% to 2.89% of the available volume within the canopy occupied by plant tissue. CLEMENTS et al. (1929: 316–317) wrote: “When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins”. CHIARUCCI et al. (2002) could therefore support Clements, concluding that with the immediate supply of canopy volume remaining over 93%, “physical space is probably never limiting by itself in terrestrial higher-plant communities, so that competition for space, distinct from competition for resources such as light, water and nutrients, is not likely to exist”.

There may be rare situations where competition for space occurs, and Clements gave radish as an example of such a species, in which the limiting organ is part root, part hypocotyl. Essentially the same situation of crowding at or below ground level occur where the organ is almost all root (e.g. carrot) or all stem (e.g. the rhizome of iris). We have no reason to suppose the results for these species would be different from those we found for the species that Clements mentioned. The below-ground community volume, the equivalent of the above-ground canopy, has never been measured and it would be extremely difficult to measure. However, since occupancy by radishes, carrots, irises etc. is maximal near the soil surface, we do not believe space in the whole rooting space would ever be more limiting than in our experiment, where after a full season of growth, right up to the commencement of bolting, the reduction that might be attributed to competition for space was by only 7.5%.

The spacing of the seeds in our experiment was intended as a compromise to maximize the opportunity for competition for hypocotyl+taproot space in the single-row plants while minimizing the opportunity for competition for light, NPK and water. The experiment had minimized light, nutrients and water resource competition by: (a) planting the seeds in a single row, or close to it, so their canopies had 10 cm to spread sideways within the box, which both shoots and roots used, (b) allowing 20 cm between the boxes to allow further expansion, which the shoots used, (c) supplying adequate amounts of mineral nutrients, both at the beginning and at intervals through the experiment and (d) ensuring that the plants were never short of water. It is also unlikely that any resource competition was different between the two treatments because the rows in the double-row treatment were only 2 cm further apart. All this suggests that the effects represent genuine competition for space, though it does leave open the possibility that competition for space, even in these most favourable conditions for it, was completely absent.

TILMAN (1982) devoted a chapter of his first book to competition for space. However, he is careful to note that physical space “may be irrelevant” and that although disturbance can create open space “it would seem better to study explicitly the resources supplied by disturbance”. Indeed. Talking of “competition for space” as a shorthand for competition for resources such as light obscures the differences between resources in the way they compete: asymmetric and therefore cumulative competition for light, soil-wide competition for nitrogen, localized competition for phosphate, etc.

Other processes can cause above-ground interference between plants, such as allelopathy, alteration of the red:far-red ratio, abrasion, most clearly seen in the gaps between tree crowns known as “crown shyness” (LONG & SMITH 1992), shaking (BIDDINGTON & DEARMAN 1985) and constraint on leaf/shoot movement (MCCONNAUGHAY & BAZZAZ 1992), but these are not types of competition by the definitions of CLEMENTS et al. (1929), BEGON et al. (1996) and GRIME (2001). Plants also interact by various means below-ground, by for example below-ground allelopathy, very speculatively electricity (SHEPHERD 1999) and signals of unknown type (GRUNTMAN & NOVOPLANSKY 2004). Although all these will, like competition for soil nutrients and water, be affected by plant spacing, none of these comprise actual competition for space. Several workers have found reduced plant growth in plants grown in small pots, an effect that could not be attributed to shortage of water or mineral nutrients (WILSON 1988b). For example, CARMÍ & HEUER (1981) investigated the role of

growth regulators in a system where bean plants were grown in very small pots. Compared to plants in larger pots, growth was reduced but S:R was increased. Water potential and nutrient concentrations were actually higher in the dwarfed plants, and application of GA and BA phytohormones removed the small-pot effect, leading the authors to conclude it was a phytohormones effect, and certainly not competition for space.

There has previously been no direct demonstration of competition for space among plants. This is hardly surprising since it seems that plant communities leave more than 95% of their space unoccupied (CHIARUCCI et al. 2002). In the present work, under the optimal conditions for finding competition for space that were specified by Clements, the reduction was only about 7.5%. Even that is not certainly attributable to competition for space, since the initial conditions could not be identical, and since the ability of the hypocotyl + taproot to spread sideways makes the mechanism for competition for space unlikely. Sideways spread of this type must happen in nature.

In real communities there will never be a monoculture of a species with tuberous roots, growing right adjacent in one dimension to maximize competition for space but spaced in the other dimension to minimize competition for light, and certainly not combined with a close-to-optimal supply of water and mineral nutrients, as used here, so it is most unlikely that a reduction of even 7.5% would be found in nature. This indicates that for all practical purposes competition for space in natural communities can be ignored. As CLEMENTS (1916) wrote: "competition for room ... seems to have no counterpart in nature".

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