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Above and Below Ground Interactions in Monoculture and Intercropping of Onion and Lettuce in Greenhouse Conditions

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Abstract

Intercropping has been seen as an advantageous strategy in sustainable agriculture. Plants however interact with one another both above and below ground with members of the same species (intraspecific) or members of a different species (interspecific) for nutrients, water and light. It is therefore essential to understand these interactions when intercropped. The objective was to examine the above and below ground interactions between onion and lettuce in monocrop and intercrop systems. We examined the various possible interactions (no competition, above ground, below ground, or full) using a full factorial randomized design under greenhouse conditions. Onion yield was highest in intraspecific above ground competition and lowest in below ground and full interspecific competition with lettuce. Dry weight of onions in above ground competition with lettuce was significantly greater than that of the control group. Fresh weight of lettuce leaves were highest in below ground and full interspecific competition treatments. The hectare model and yield results suggest that there is strong below ground competitive effect between onion and lettuce in intercrop. Asymetric interspecific facilitation was found: facilitation by onion led to increased lettuce yield but a negative effect of lettuce on onion yield was observed. Knowledge of competitive interactions between component crops can have several applications in sustainable agricultural as it helps to match the most efficient species under specific conditions.

Keywords

Intraspecific and Interspecific Competition, Onion, Lettuce, Sustainable Agriculture, Facilitation

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1. Introduction

Intercropping is an agricultural technique based on the management of plant interactions to maximize crop yield and involves cultivating two or more crops in the same field within the same growing season [1] [2]. Intercropping can provide increased yields in an environmentally sustainable manner through resource complementarity, since niche overlap and competition between species is assumed to be reduced, permitting crops to capture a greater range and quantity of resources than in monoculture [3] [4].

Competitive interactions between two plants, brought about by a shared requirement for soil nutrients, water or light, can have negative effects on either species by decreasing growth rate, survival, reproduction or yield of one or both plants [5] [6]. In intercropping, the net effect of competition includes not only interspecific competition but also intraspecific competition [3]. In addition, competition can be above ground when plants modify their leaf areas in function of light interception, or below ground when plants alter the length, density, and spatial distribution of their roots in response to the presence of a neighbour [1] [6]. Lettuce (*Lactuca sativa*), for example, is expected to be more competitive in intercrop because it is a fast emerging, tall and broad-leaf plant that is able to obtain a larger share of available light than slower growing and smaller plants like onion [7]. Indeed, onion crops (*Allium cepa*) are known to be a weak competitor because of their initial slow growth rate after planting (juvenile growth), development of shallow fibrous roots and a small above ground canopy, which does not cover the soil [7].

In order to study competition in intercrop treatments and fully explore the yield potential of intercrops, we must examine and distinguish between the different types of interactions [3]. The cumulative and individual effects of above and below ground competition are not predictable; they vary with availability of resources and the species used [1]. Only by physically separating above ground competition from below ground competition can we distinguish between competition for light and competition for nutrients and water.

Research into cereal-legume intercrops is extensive and common in tropical and subtropical regions such as Africa and Asia. There is however limited research dedicated to vegetable or non-legume intercrops, intercrop competition and the specific interactions occurring between intercropped species, especially in temperate regions [2] [8] [9]. The objective of this experiment was to examine the interactions between onion and lettuce in monocultures and intercrops to determine whether the interactions were above or below ground, interspecific or intraspecific in nature, and if the interactions were positive (facilitative) or negative (competitive). It is hypothesized that the biomass for lettuce and onion intercrops will be greater than that of the monocultures. From this, we expect that intraspecific competition between lettuce plants will occur mainly above ground while interspecific competition between lettuce and onion will occur mainly below ground. Intraspecific competition between onions will be limited to minimal below ground interactions, while the biomass of onion plants in above ground competition with lettuce is expected to be negatively affected.

2. Materials and Method

2.1. Experimental Design

We used a complete random factorial design in a greenhouse setup where both intraspecific and interspecific competitions were examined using 11 treatments with 10 replicates: one single plant of onion 1) or lettuce 2) acted as the control groups; two plants of onion 3) or of lettuce 4) or one onion and one lettuce 5) planted in the same pot with full (above and below ground) interactions; two plants of onion 6) or of lettuce 7) or one onion and one lettuce 8) planted in a pot where the above ground portions were separated with greenhouse plastic (no above ground interaction); and two plants of onion 9) or of lettuce 10) or one onion and one lettuce 11) planted in two different pots but placed side by side (no below ground interaction). Seeds were sown directly into pots: onion at a depth of 2 cm and lettuce at a depth of 1 cm (according to the seed company). Seeds were spaced approximately 10 cm from each other in either the same pot for below ground and full competition, or in two pots for above ground competition treatments (one per pot) (note that the volume of soil was the same for all plants, whether in a larger pots for two plants or smaller pots for single plants). Plants were watered when the soil was dry to the touch. Fertilizer (20-20-20) was mixed into the water once every two weeks. Temperature varied between 15˚C and 25˚C with photoperiod of 14 h day/10 h night.

Lettuce was harvested after 55 days (on May 1, 2013). Fresh leaves were weighed and the samples were placed into a drying cabinet at 45˚C for two weeks, at which point dry weight was recorded for each sample. The onion plants were left to grow for another 33 days and were harvested on June 3 - 4, 2013. Fresh bulb weight was immediately recorded, samples were placed in the drying cabinet, and after two weeks the dry onion samples were removed from the oven and weighed.

2.2. Data Analyses

Fresh and dry weight data were transformed using a natural logarithmic transformation to satisfy normality and compared between treatment groups with an analysis of variance followed by a multiple range Dunnett T3 post-hoc test.

A model was created to estimate the yield of lettuce and onion in intercrop and monoculture in a simulated area of 1 hectare (100 m × 100 m). The hectare model uses average yield from both the onion and lettuce, controls, intraspecific full competition and interspecific full competition treatments. In the onion monoculture model, rows were spaced 40 cm apart, and onion plants were spaced 10 cm apart within rows, in accordance with onion-growing fact sheet [10]. In the lettuce monoculture model, lettuce rows were spaced 30 cm apart and plants were spaced 25 cm apart within rows. In the intercrop model, onion and lettuce were alternated every 12 cm with 30 cm between rows. Values were compared using a standard normal distribution (z-test).

The Relative Interaction Index (RII, [11]) was used to determine the types of interactions occur-ring between species in each treatment group. The fresh weight of onion bulbs and lettuce leaves were compared to their respective control groups using the following Equation (1):

$$\text{RII}=\frac{\text{Mw}-\text{Mo}}{\text{Mw}+\text{Mo}}$$

where Mw is the fresh mass of plant matter (lettuce leaves or onion bulbs) in competition with neighbours, and Mo is the fresh mass of isolated plants (control). RII has values ranging from −1 to 1, is symmetrical around zero and is negative for competition and positive for facilitation [11]. Given a 95% confidence interval, a treatment was considered competitive if the RII value was less than −0.10, facilitative if the RII value was greater than 0.10, and neutral if the RII value was between −0.10 and 0.10 [11]. All statistical tests were performed using SPSS version 17.0.

3. Results

3.1. Biomass and Yield Analyses-Onions

Onion bulbs exposed to intraspecific above ground competition had the highest fresh weight. In interspecific competition, fresh bulb weight was the lowest in below ground and full competition with lettuce (**Figure 1**). Onions in interspecific below ground and full competition had significantly lower dry weight of bulbs than the onion control group, while onions growing in intraspecific above ground competition had the largest dry weight of bulbs (**Figure 2**). Additionally, onions in above ground competition with lettuce had significantly greater dry weight of bulbs than those in the control group.

When individual onions were grown in pots, *i.e.* with no competition, and extrapolated for yield in a field of 1 hectare, the results predicted the highest yield with a mean of 247 kg/ha (**Figure 3**). However, the mean value decreased to 185 kg/ha (**Figure 3**) as soon as two onions grown in the same pot (simulating intraspecific monoculture) were considered. While this value considered the same spacing, it is clear that there is an interaction between individuals. The lowest yield is predicted when onions are planted in interspecific competition with lettuce (63 kg/ha, **Figure 3**). This value was statistically different than the monoculture yields ($p < 0.001$).

3.2. Biomass and Yield Analyses-Lettuce

Lettuce yield was greatest in below ground and full interspecific competition with onion compared to intraspecific or no competition (**Figure 4** and **Figure 5**). The hectare model for lettuce showed no significant difference between lettuce in individual pots (control) and in monocultures ($p = 0.464$, 6850 kg/ha, 6893 kg/ha) (**Figure 3**). The yield of lettuce in interspecific competition with onion in the hectare model was both the highest lettuce yield observed, and statistically different than the yield of the monoculture models ($p = 0.012$, 9821 kg/ha) (**Figure 3**).

3.3. Competition vs Facilitation

The effect of lettuce on onion was competitive in the below ground and full competition treatments, but was

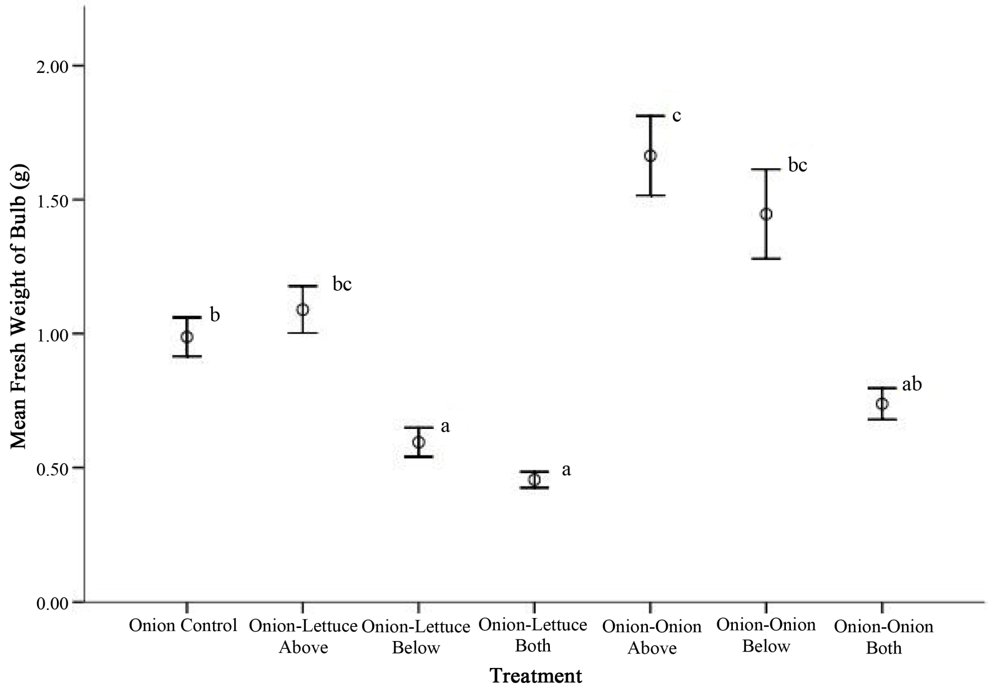

Figure 1. Average fresh weight of onion bulbs grown in control, intraspecific or interspecific competition with lettuce. An analysis of variance with a Dunnett T3 Post-hoc test was used to find significance between treatments. Letters next to the standard error bars note significance df = 6, MS = 2.62, F = 17.04, p < 0.001).

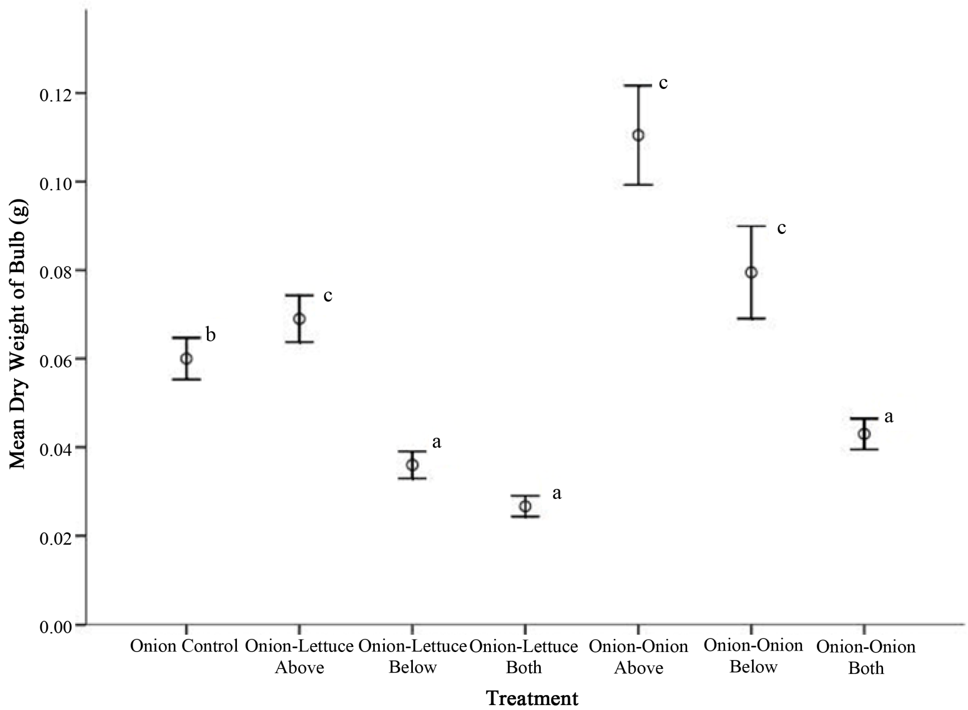

Figure 2. Comparison of average dry weight of onion bulbs grown in control, or competition with lettuce or onion. Significance between treatments is represented using letters next to the standard error bars, and was found using an analysis of variance with a Dunnett T3 Post-hoc test (df = 6, MS = 2.82, F = 13.94, p < 0.001).

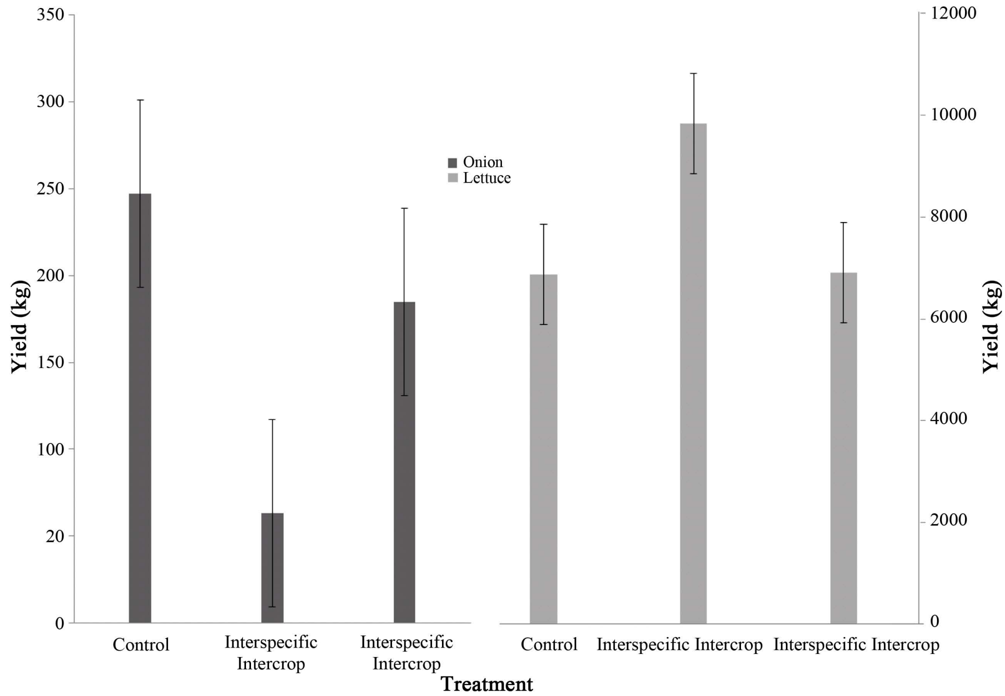

Figure 3. Predicted yield comparison of onion bulbs (kg/ha) for onion grown in monoculture assuming no competition, onion grown in monoculture with intraspecific competition and onions grown in an intercrop under interspecific competition with lettuce. Error bars are +/−1 standard error.

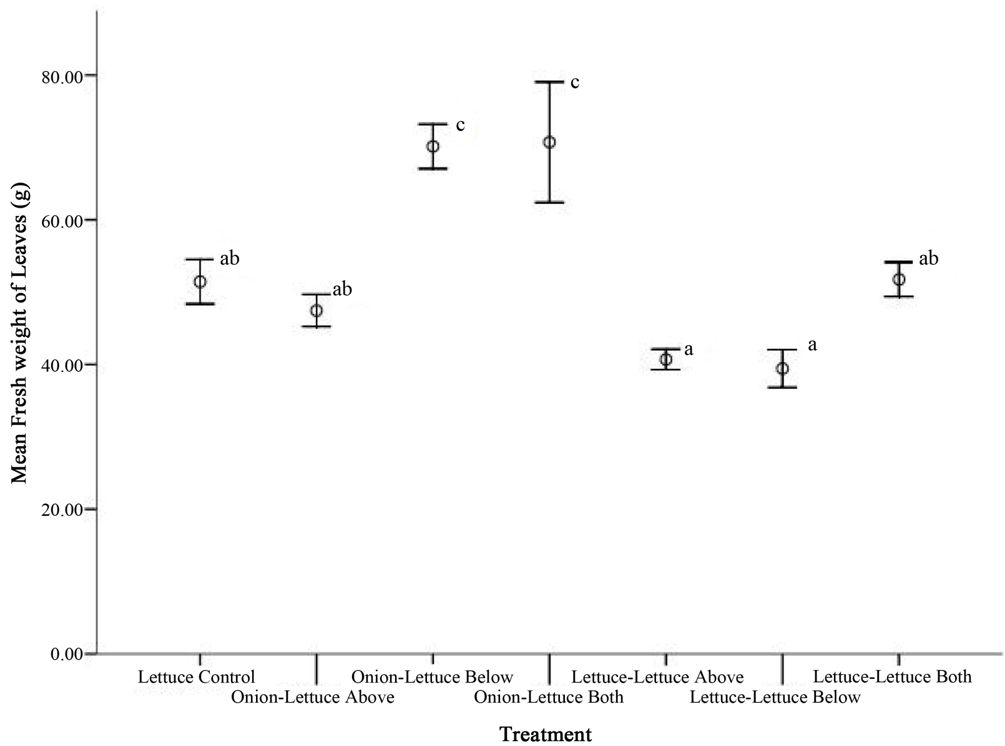

Figure 4. Comparison of average fresh weight of lettuce leaves growing in control and intraspecific and interspecific competition with onion. Significance was determined using analysis of variance with a Dunnett T3 post-hoc test, and is represented using letters adjacent to the standard error bars (df = 6, MS = 0.69, F = 10.50, $p < 0.001$).

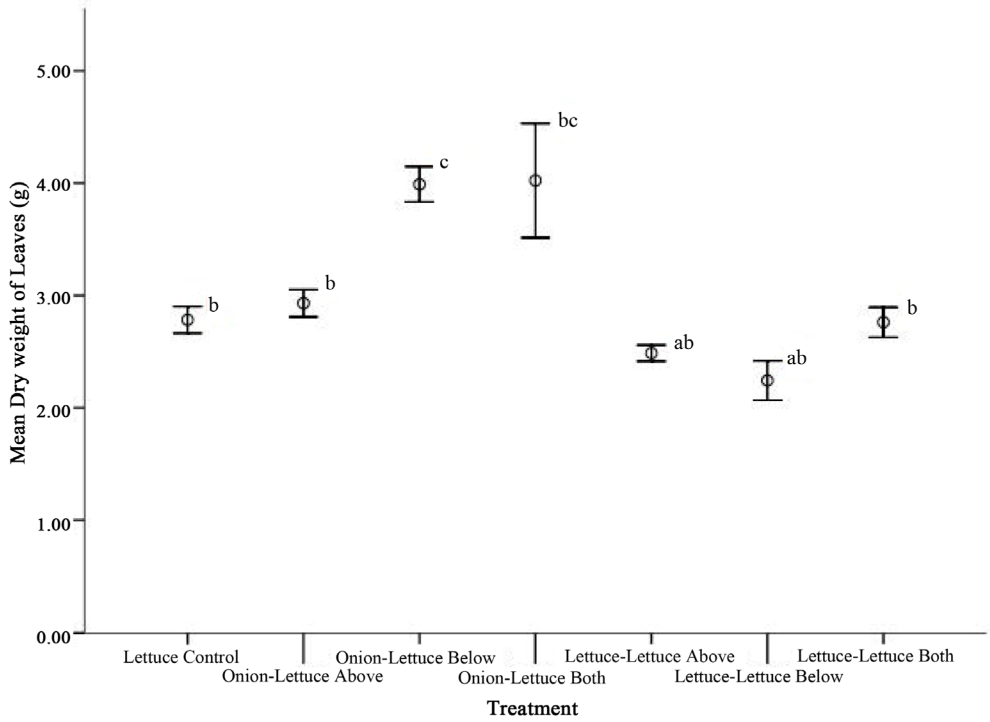

Figure 5. Average dry weight of lettuce leaves for lettuce grown in control, intraspecific or interspecific competition with onion. Letters beside error bars signify significance between treatments found using analysis of variance with a Dunnett T3 post-hoc test (df = 6, MS = 0.63, F = 8.67, $p < 0.001$).

neutral in the above ground competition treatment. Onion monoculture was facilitative in above ground interacttion as well as below ground interaction, but when paired in full competition, the effects were slightly competitive (**Table 1(a)**).

When lettuce was paired with onion above ground, there was a neutral effect, while a facilitative effect was observed when lettuce was paired with onion in below ground and full interaction treatments. The effects of lettuce in intraspecific interaction above ground and below ground were competitive, while there was a neutral effect for lettuce paired with lettuce in full interaction (**Table 1(b)**).

4. Discussion

Competitive interactions among plants of the same or different species can have either a positive or a negative effect on growth, reproduction, and survival [1] [5]. In this study, we hypothesized that the biomass for lettuce and onion intercrops would be greater than that of the monocultures. Indeed, for lettuce, we found that the biomass in intercrops with onion was generally greater than in monoculture. However, we also found that the yield of onion bulbs in all cases of intercrop with lettuce was equal to or lower than the biomass of monocultures. These results are especially visible in the predicted yield (hectare) model. It is known that onions are usually not very competitive against weeds or crops that are planted and growing at relatively the same time because of its slow growing habit [12]. Even once the lettuce removed, the recovery of onion in growth (measure in terms of plant height) was not significant (data not shown).

This unbalanced benefit of both crops in intercropping has been previously observed, showing the complexity of the system and its interactions [2]. Similar results were observed in a leek/celery inter-crop mixture where total yield was equal to the yield in the two species in monoculture, but celery competition reduced leek yield and quality [13]. In a cabbage/radish intercrop, yield of cabbage was significantly less in intercrop compared to monoculture [14]. This is known as asymmetric interspecific facilitation where the intercrop combination increases the yield of one species, but causes a decrease in the other [15].

The results suggested that the interactions were not necessarily similar for above and below ground. In interspecific competition, onions faired best in above ground interaction with lettuce. We expected that lettuce plants would shadow

Table 1. Mean fresh weight of plant tissue (g), Relative Interaction Index (RII) values and type of interaction defined by RII for (a) onions when in intraspecific or interspecific competition with lettuce and (b) lettuce when in intraspecific or interspecific competition with onion.

(a)

Treatment	Fresh Bulb Weight (g)	RII	Interaction
Onion Control	0.99		
Onion-Onion Above	1.66	0.25	Facilitative
Onion-Lettuce Above	1.09	0.05	Neutral
Onion-Onion Below	1.45	0.19	Facilitative
Onion-Lettuce Below	0.59	−0.25	Competitive
Onion-Onion Both	0.74	−0.14	Slightly Competitive
Onion-Lettuce Both	0.45	−0.38	Competitive

(b)

Treatment	Fresh Leaf Weight (g)	RII	Interaction
Lettuce Control	51.47		
Lettuce-Lettuce Above	40.68	−0.12	Facilitative
Onion-Lettuce Above	47.44	−0.04	Neutral
Lettuce-Lettuce Below	39.43	−0.13	Facilitative
Lettuce-Onion Below	70.13	0.15	Competitive
Lettuce-Lettuce Both	51.75	0.00	Slightly Competitive
Lettuce-Onion Both	70.71	0.16	Competitive

onions, but it appears that below ground competition with lettuce limited onion growth more than above ground competition. The combined effect of full competition is therefore dominated by the below ground portion. A similar reduction of onion bulb yield due to intercropping with vegetables was noted by [16].

Our comparison between individual onion and onion in full or below ground competition also suggest that onions required greater spacing than what was stated by the seed company due to mainly below ground effect. Our results were similar to Peach *et al.* [17] who reported that intraspecific onion yield was improved by eliminating either above or below ground competition, but full competition greatly reduced yield. Aerts *et al.* [18] also found similar results.

It was expected that broader and more horizontal leaves of lettuce would lead to increased shading, as well as respiration and maintenance costs, thus likely reducing yield in intraspecific above ground competition [7] [19]. However, this was not necessarily the case; suggesting that light competition, at least at the soil surface, was not as much as a factor as expected [5].

Intercropping has been shown to have yield advantage presumably resulting from both above and below ground facilitation between intercropped species [15]. Contrary to our initial hypothesis, the RII of onion showed a facilitative effect in intraspecific above and below ground competition. In intercropping, onion played a neutral to facilitative role in the presence of lettuce. RII results for lettuce showed that in monoculture, neutral or slightly competitive effects would be found. The extensive root system of lettuce most likely exploited a large soil volume, contributing to its high interspecific competitive ability below ground, thus limiting soil moisture and nutrient availability for onions [20].

In the face of interactions or changes in environmental cues, plants can respond by emitting different biogenic volatile organic compounds or by modifying their internal hormonal balance [21]. Allelochemicals have been found to influence interactions between plants of different species thus reducing or improving their productivity potential [2]. While this aspect was not considered in this study, we can assume that some chemical interactions might have influenced plant responses and performance. The facilitative outcome observed in lettuce in interspecific below ground competition with onions may be due to the excretion of certain allelopathic chemicals such as growth promoting compounds [22] [23]. It may be interesting to consider these chemicals (most likely allelochemicals) in future studies.

Results from this study have promising applications in crop yield optimization and sustainable agriculture. While intercropping has been practiced in some countries for centuries, several questions remain unanswered regarding optimization of plant combinations, optimal density, spatial arrangements, or selective breeding necessary to produce maximum yields in full scale agricultural systems [2] [3]. Field testing, as mentioned in [2] will also be required to examine the influence of weeds and pests in such systems and determine whether allelochemicals from other species like weeds can affect the outcomes.

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