Impact of regular mowing, mowing height and grass competition on tuber number and tuber size of yellow nutsedge clonal populations (*Cyperus esculentus* L.)

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Abstract

Cyperus esculentus, a perennial sedge, is one of the most dangerous weeds in agriculture because of its high multiplication potential, its high risk of tuber spread and its low sensitivity to control measures. To diminish the risk of *C. esculentus* spread and incursion into adjacent crops by creeping rhizomes, control measures should also focus on non-cropped areas adjacent to these crop zones. Defoliation by mowing is an example of one of these control measures. The aim of this study was to identify the critical mowing interval and height required for preventing tuber formation and to assess the combined effect of mowing and competition exerted by the grassy vegetation on the growth and spread of *C. esculentus* in field margins. In two separate years we conducted an indoor container (11 L) experiment, under a worst-case scenario, in which genetically distinct clones, grown alone or in combination with *Lolium perenne*, were subjected to season-long mowing regimes that differed in mowing interval (1-, 2-, 4-, and 8-weeks) and/or mowing height (2 and 5 cm). Weekly and 2-weekly mowing at 5 cm within an 18-week period significantly reduced tuber production of *C. esculentus* grown with competition (up to 93 and 98% reduction in tuber number respectively) and without competition from *L. perenne* (both a 97% reduction), compared to the uncut control with and without competition, respectively. Compared to a mowing height of 5 cm, a mowing height of 2 cm resulted in better control of *C. esculentus*, with tuber numbers up to 32% lower and 5-65% lighter. 2-weekly mowing at 2 cm height can be an effective strategy for containing or reducing *C. esculentus* patches in field margins.

KEYWORDS

Cutting, clone, field margins, herbaceous strips, herbicide-free areas, mechanical weed control, *Lolium perenne*

1 INTRODUCTION

Cyperus esculentus L. (yellow nutsedge), a perennial sedge, is one of the most dangerous weeds in agriculture because of its high multiplication potential, its high risk of tuber spread with machines and vehicles, and its low sensitivity to control measures. In Belgium, *C. esculentus* is found in almost all arable crops and has infected over 50 000 hectares of the 1 367 000 ha of cropland available in Belgium (Waarnemingen.be, 2023). In addition, several infestations are also found in semi-natural, and natural habitats adjacent to croplands e.g., roadsides, neglected areas, and banks of irrigation canals and streams. Control is enforced via Integrated Pest Management (IPM) specifications and obligatory weed control (Departement Landbouw & Visserij, 2019). An integrated strategy, sustained over years, is necessary and should include the prevention of spread and a combination of cultural, mechanical, and chemical control methods as none of these measures alone is sufficiently effective (De Ryck et al., 2021; Schröder et al., 2021). Control strategies aim to deplete the bud bank, by preventing the formation of new tubers and killing the present tubers (De Cauwer et al., 2017; Bohren and Wirth, 2018). In cropped areas, *C. esculentus* can be controlled by using individual or combinations of treatments with herbicides, regular soil cultivation, and competition (De Cauwer et al., 2017; Schröder et al., 2021). To diminish the risk of *C. esculentus* spread and incursion into adjacent crops by creeping rhizomes, control measures should also focus on non-cropped areas adjacent to these crop zones. However, in non-cropped areas fewer control options are available. In order to reduce pesticide contamination of surface waters and to minimize negative environmental impact, chemical control measures are not allowed in the EU in a lot of zones such as ditches, pre-existing semi-natural field boundaries, roadside verges, crop-free zones (i.e., 1-m-wide herbaceous strips between the last crop row and the top of the bank of a surface water), pesticide-free zones (i.e., 3 m wide strip adjacent to a water course) and spray-free buffer zones of varying width depending on pesticide choice and drift reducing technology (Huijsmans and van de Zande, 2011). In many of these zones, tillage is also not permitted (e.g., crop-free buffer zones) or is impractical. Hence, aside from thermal weed control options (e.g. steaming and electroweeding), mowing and competition are the sole legal or practically feasible control options for large *C. esculentus* infestations in these non-crop areas. In pastures and meadows, chemical control and tillage options targeting *C. esculentus* are also not possible due to a lack of selectivity with desired crop and pasture species.

Like many perennial weeds, *C. esculentus* plants may survive defoliation (i.e., destruction of aboveground plant parts) by two main strategies: (1) avoidance and (2) reshoot potential. Growing close to the ground helps plants avoid losing all aboveground biomass to mowing (e.g., *Taraxacum* spp.). Fortunately, *C. esculentus* has a stemmy growth habit and may lose a substantial proportion of its shoot biomass with each defoliation. However, *C. esculentus* may easily regrow/resprout from the apical or axillary buds of the basal bulb located just beneath the soil surface. When shoots are cut below the soil surface (hoeing) new shoots may arise through resprouting from axillary buds on the mother tuber or creeping rhizomes. In case of partial or complete removal of green parts, resprouting and regrowth capacity will depend on energy reserves in belowground structures and tuber weight in particular, as large tubers possess more axillary buds and storage tissue (Stoller et al., 1972; Stoller and Wax, 1973; Santos et al., 1997a).

Only a few studies have investigated the effects of repeated defoliation or mowing on *C. esculentus*. According to Thullen and Keeley (1975), complete removal of *C. esculentus* shoots at 2-week intervals allowed sprouting of other buds on the tuber. However, removal at 4-week intervals reduced new sprout numbers and decreased tuber longevity. According to Summerlin et al. (2000), frequent mowing at low heights is an effective way to reduce *C. esculentus* populations. Season-long mowing (14-18 weeks) at 1.3 and 3.8 cm with mowing frequencies of three times per week and once a week respectively, completely inhibited tuber production, and reduced shoot number by 94 and 74%. These mowing regimes also reduced spread by 84 and 67% under the 1.3 and 3.8 cm mowing regimes, respectively. However, such intensive mowing regimes (1.3-cm regime in particular) may be suitable for maintaining golf course fairways and greens but not for managing herbaceous field margin strips, pre-existing field boundaries, grassy strips, or agricultural grasslands. Indeed, herbaceous vegetations alongside cropped areas are mown less intensively and use disc, flail or scythe mowers at higher mowing heights of 3.8-7.0 cm. None of these studies identified the critical mowing interval (mowing frequency) required for preventing tuber formation nor assessed the combined effect of mowing and competition exerted by the grassy vegetation on the growth and spread of *C. esculentus*.

Cyperus esculentus is sensitive to shading (Keeley and Thullen, 1978; Lotz et al., 1991; Santos et al., 1997b; Li et al., 2001a), soil fertility and soil moisture (Li et al., 2001b; Ransom et al., 2009). On cropland, competition with competitive crops or cover crops such as oil radish (*Raphanus sativus* ssp. *oleiferus* (Stokes) Metzger) suppressed surviving plants and reduced the formation of tubers significantly (Bohren and Wirth, 2015). To what extent grassy vegetation of field boundaries or field margin strips can contribute to *C. esculentus* control is poorly documented and will likely depend on soil nutrient and moisture status, vegetation composition, and vegetation management, in particular mowing frequency and mowing height. Mowing height and frequency may indeed affect interspecific competition between co-occurring grassland species (Le Bagousse-Pinguet et al., 2012). Many grasses respond to mowing with increased tillering (Brink et al., 2014), though this response may be reduced by interspecific competition (Kolberg et al., 2018) and lower cutting heights (Brink et al., 2013).

Thus, our objectives were to find out 1) which defoliation strategies (combination of mowing height and mowing interval) are most effective for controlling *C. esculentus* clones differing in tuber size, 2) whether competition exerted by the grassy vegetation can complement control efficacy of regular mowing, and 3) if the clonal population affects the control efficacy of mowing and competition.

2 MATERIALS AND METHODS

2.1 Experiments

2.1.1 Experimental factors

We conducted two mowing experiments, both with different clones of *C. esculentus* to compare the control efficacy of mowing regimes. The clones (tubers) were collected from different heavily infested fields (*C. esculentus* coverage of >20%) in Belgium and named after the location where they were collected. They are genetically and morphologically distinct *C. esculentus* populations (De Ryck et al., 2023).

Experiment 1, conducted in 2018, was a combination of three clones, two tuber sizes, two levels of grass competition and five mowing intervals. The clones selected were 'Desselgem', 'Oostkamp', and 'Waregem 2', with an average individual tuber fresh weight of 557 ± 26, 682 ± 29, and 634 ± 23 mg, respectively. Tubers were planted on April 27 (i.e. around the time most tubers begin to sprout under natural Belgian outdoor conditions). To assess the impact of tuber size on efficacy of regular mowing, each clone was established from two tuber weight categories (300-400 mg and 600-700 mg). Plants were grown alone (no interspecific competition) or in competition with *Lolium perenne* L. 'Melonora' (perennial ryegrass) sown on April 27 at a density of 1920 seeds m^{-2} (120 seeds pot^{-1}). *Lolium perenne* was chosen as a competitor as it is a major grass species in field boundary vegetations and grass buffer strips in or along arable fields in Belgium. Plants were left unmown or were mown at 1-, 2-, 4-, and 8-weekly intervals, resulting in 17, 9, 5, and 3 mowing passes, respectively, over an 18-week monitoring period starting on May 28 (first cut, performed at the 8-leaf stage of *C. esculentus*) and ending on September 17 (last cut). Mowing height was set at 5 cm above the substrate i.e., the common mowing height for roadside or field boundary vegetation management. After the last cut at the end of September, most *C. esculentus* shoots died back to the ground.

Experiment 2 was conducted in 2020 to support the results obtained in experiment 1 and to test an extra mowing height. The experiment was a combination of two different clones, two competition levels and eight mowing regimes. We used clones 'Oostkamp' and 'Waregem 2' (average individual tuber fresh weight was 474 ± 10 and 316 ± 20 mg, respectively). Tubers were planted on May 5. As in experiment 1, plants were grown alone (no interspecific competition) or in competition with *L. perenne* 'Melonora' sown (May 5) at a density of 1920 seeds m^{-2} (120 seeds pot^{-1}). The mowing regimes comprised all combinations of four mowing intervals [1-, 2-, 4-, and 8-weekly resulting in 17, 9, 5, and 3 mowing passes, respectively, over an 18-week monitoring period starting on June 8 (first cut, performed at the 8-leaf stage of *C. esculentus*) and ending on September 28 (last cut)] and two mowing heights (2 and 5 cm), representing various levels of defoliation, and one uncut control. Mowing heights of 2 and 5 cm are frequently applied for lawn and grass strip management. After the last cut at the end of September, most *C. esculentus* shoots died back to the ground.

2.1.2 Experimental setup

Treatment combinations of clones, competition levels and mowing regime effects on *C. esculentus* were compared in pot experiments that were arranged in a randomized complete block design with four replicates. Pots were filled with steam sterilized sandy loam containing 2.6% organic matter, 46.7% silt (2-50µm), 43.4 % sand (>50 µm), and 10.0% clay with a pH-KCl of 5.5. Soil steam sterilisation was performed with a Sterilo 7k earth steamer (Harter elektrotechnik, Schenkenzell, Germany) to avoid any weed interference with *C. esculentus* and *L. perenne*. The tubers used as planting material were produced in the year preceding the start of the experiments and kept in a fridge (5°C) from harvest until planting. In 2018, tubers were selected according to the predetermined tuber weight categories as mentioned above. In experiment 2, only average-sized tubers were used as the results from experiment 1 indicated no effect of tuber size on all tested plant responses: average-sized tubers were defined as tubers with a fresh weight falling between 80 and 120% of the clone-specific average fresh tuber weight.

In both experiments, the experimental unit was an 11 L (25 x 25 x 26 cm) pot with *C. esculentus* plants originating from five (experiment 1) and eight (experiment 2) pregerminated tubers of a particular clone, growing in presence or absence of *L. perenne* plants. These tuber numbers correspond to 0.45 and 0.73 tubers per litre soil respectively and are in line with tuber densities (median of 0.86 tubers per litre soil) found by Bohren et al. (2018) in moderately to highly infested patches. The tubers were planted, evenly spread out, at a depth of 4 cm. In pots with grass competition, 120 *L. perenne* seeds were evenly distributed over the pot surface and covered with 5 mm of soil substrate. Pots were placed under a rain shelter greenhouse and optimally irrigated by overhead sprinklers at a rate of 2.5 to 3.8 mm day^{-1} depending on daily water evapotranspiration. As most semi natural field boundary vegetations and grass strips are not fertilised, pots received no fertilisation. The mowing moments, daily global radiation, and min. and max. daily temperatures for each year, measured by the nearby meteorological station, are given in Figure 1.

Figure 1 near here.

2.2 Measurements

Shoot number was determined on the day of the last cut. At the end of the shoot senescence (BBCH stage 97) of *C. esculentus* (late October), the following belowground plant responses were measured or calculated: number of newly produced firm tubers, fresh tuber weight and fresh individual tuber weight. Hereto, the newly formed tubers (mature and immature tubers with a diameter of > 2 mm) were washed out of the pot substrate on a 200 µm sieve, cleaned, counted, and weighed. Before counting and weighing, all non-firm or glassy tubers that burst open when slightly squeezed between thumb and index finger were removed. The fresh individual tuber weight was calculated as the fresh tuber weight divided by the number of newly formed tubers.

2.3 Statistical analysis

All data were analysed in R version 4.1.2 (R Core Team, 2021). To determine if the data from both pot experiments can be combined for analysis, four-way ANOVA's with clone, mowing interval, competition and year as factors were performed on plant response data from all combinations of two clones ('Oostkamp' and 'Waregem 2'), five mowing intervals, two competition levels, and two years (2018 and 2020) (i.e. the common experimental part). Four-way ANOVA's indicated that all plant response variables (tuber and shoot number, fresh tuber weight, and fresh individual tuber weight) were significantly affected by high-order interactions [two- ($p < 0.001$), three- ($p < 0.01$), and four-way ($p < 0.01$) interactions] including the independent variable year. Therefore, the dataset was split according to year for further analysis and reporting, meaning that the pot experiments were analysed separately.

In experiment 1, all data were analysed using parametric tests run at the 5% significance level. A four-way ANOVA (three clones x five mowing intervals x two competition levels x two tuber sizes) was used to check for interactions. The ANOVA-model was reduced until only significant terms remain. Homoscedasticity and normality assumptions were checked with the Levene-test and a QQ-plot, respectively. To check for significant differences the Tukey-HSD method was used.

The statistical analysis of experiment 2 was the same as for experiment 1. The four-way ANOVA compromised two clones, five mowing intervals, two mowing heights, and two competition levels.

The full model with all main effects and interaction terms and their significances is given in Tables 1 and 2 for experiment 1 and 2 respectively. In experiment 1, a significant two-way interaction was present between mowing interval and competition level ($p < 0.001$) for tuber and shoot number and fresh tuber weight and between mowing interval and clone ($p < 0.05$) for the fresh individual tuber weight. Clone had a significant effect on tuber ($p < 0.01$) and shoot number ($p < 0.05$) and competition had a significant effect on fresh individual tuber weight ($p < 0.01$). There was no effect of tuber size nor was tuber size involved in a significant interaction. In experiment 2, there was a significant two-way interaction between mowing interval and competition for tuber ($p < 0.001$) and shoot number ($p < 0.01$) and for fresh tuber weight ($p < 0.001$) as well as between mowing interval and clone ($p < 0.05$) for tuber number, between competition and clone for tuber ($p < 0.01$) and shoot number ($p < 0.05$), between competition and mowing height for tuber ($p < 0.001$) and shoot number ($p < 0.01$), and between mowing interval and mowing height for fresh individual tuber weight ($p < 0.01$) and shoot number ($p < 0.001$).

Table 1 and 2 near here

3 RESULTS

The results are described following the order of the three objectives. These sections report the effect of mowing, the effect of competition, and the effect of clone. Within each section, the effects on each parameter are described according to the significant interactions reported in section 2.3. The results of both experiments are reported together wherever possible. Low numbers of new *C. esculentus* tubers (i.e. <5 and <8 per pot in experiment 1 and 2, respectively) at the end of the growing season (late October) clearly indicate a decrease in infestation as none of the original tubers were alive at this time. Percent decreases reported hereafter are expressed relative to the mean of uncut control pots. In both experiments, a majority of the tubers extracted from pots under weekly and 2-weekly mowing intervals were immature (whitish tuber skin) or glassy. These pots also contained fully resorbed tubers. As mentioned earlier, glassy tubers that burst open under slight pressure were not included in the tuber number.

3.1 Effect of mowing

Reduced mowing intervals lowered ($p < 0.001$, Tables 1 and 2) all *C. esculentus* growth parameters assessed. In absence of competition, tuber numbers obtained under the weekly and 2-weekly mowing intervals, repeated during the full length of the growing season, were lower (25 and 22 tubers for experiment 1 and 80 and 146 for experiment 2, respectively) than tuber numbers under the 4- and 8-weekly mowing intervals but were not different ($p > 0.05$) from one another (Figure 2). For experiment 1, the weekly and 2-weekly mowing intervals had lower shoot numbers (32.6 and 41.6 shoots, respectively) than the other mowing intervals (60.3, 56.7, and 61.2 shoots for the control, 8-, and 4-weekly mowing interval, respectively) (Figure 3A). However, in experiment 2 only the weekly mowing interval had lower shoot numbers (up to 30%) than the other mowing intervals (Figure 3B). Without competition, the weekly mowing intervals lead to a reduction of 99.8 and 96% in fresh tuber weight for experiment 1 and 2, respectively (Figure 4). The fresh individual tuber weight was lower under a 1- and 2-weekly mowing interval than under the other mowing intervals (Figure 4).

A lower mowing height decreased the shoot number and the fresh individual tuber weight ($p < 0.001$, Table 2) but not the fresh tuber weight ($p > 0.05$). The number of shoots was only reduced by the mowing height when mown weekly (15.8 shoots at a height of 2 cm versus 33.5 shoots at a height of 5 cm) (Figure 5B). Fresh individual tuber weight was 0.9 to 2.8 times heavier under the 5 cm mowing height as compared to the 2 cm mowing height (Figure 6). For each mowing height, the greatest reduction in fresh individual tuber weight was obtained under the weekly mowing interval, namely 89% at 2 cm height and 67% at 5 cm height (Figure 6). When mown, the fresh individual tuber weight was 5 (8-weekly) to 65% (weekly) lower under a 2 cm mowing height versus a 5 cm mowing height (Figure 6).

Figures 2, 3, 4, 5, and 6 near here.

3.2 Effect of competition

The combination of mowing and competition lowered ($p < 0.001$, Tables 1 and 2) all the assessed *C. esculentus* growth parameters. Within each mowing interval, the treatments with *L. perenne* competition had lower tuber numbers than the treatments without competition (Figure 2). Treatments with competition produced 2.5 to 7.1 times fewer tubers than when grown without a competitor in experiment 1 and 4.2 to 5.6 times less tubers in experiment 2 (Figure 2). The control (no cuts) with competition produced 5.3 and 4.4 times less tubers than the control without competition in experiment 1 and 2 respectively (Figure 2). Within both competition levels, maximum reductions in tuber number relative to the uncut control were achieved under the 2-weekly mowing interval in experiment 1 (98 and 97% with and without competition, respectively) and under the weekly interval in experiment 2 (90 and 89% with and without competition, respectively), albeit not different ($p > 0.05$) from reductions under the 2-weekly mowing interval (Figure 2). Fresh tuber weight was affected by competition and was 3.5 to 9.7 times (experiment 1, Figure 4A) and 4.3 to 5.7 times (experiment 2, Figure 4B) lower with competition than without competition, irrespective of mowing interval.

Under competition with *L. perenne*, the 2-weekly mowing interval resulted in the largest reduction in tuber numbers in experiment 1: it reduced tuber numbers with 98% (compared to the uncut control with competition), up to 3.1 tubers (Figure 2A). While in experiment 2, weekly mowing resulted in the lowest tuber numbers (90% reduction, 16.7 tubers) (Figure 2B). However, these reductions were not different ($p > 0.05$) from that of the weekly mowing interval. Overall in experiment 1, only the combination of competition with *L. perenne* and a 2-weekly mowing interval at 5 cm achieved a decrease in soil tuber density (less than 5 new tubers produced). This decrease was not achieved in experiment 2. In both experiments, mowing interval did not affect shoot number in the presence of *L. perenne* (10.5 to 17.6 shoots and 9.1 to 15.1 shoots for experiment 1 and 2 respectively) (Figure 3). With competition, the 2-weekly mowing interval (0.10 g, experiment 1) and weekly mowing interval (1.7 g, experiment 2) achieved the lowest fresh tuber weight but were not different ($p > 0.05$) from the other mowing intervals, apart from the control (Figure 4). These weights correspond to a reduction in fresh tuber weight of 99.8 and 96.9% for experiment 1 and 2 respectively. With competition, the average fresh individual tuber weight was lower (18%) than without competition (0.168 ± 0.015 vs. 0.206 ± 0.016 g).

There was a significant ($p < 0.001$) interaction between mowing height and competition level for the tuber number (Figure 7C). Without competition, the tuber production at a mowing height of 2 cm was 32% lower than the tuber production at a 5 cm mowing height. With competition, the tuber production was not affected by mowing height (Figure 7C). The tuber production was 3.6 or 5.7 times lower under competition than under no competition, for the 2 and 5 cm mowing heights, respectively (Figure 7C). In experiment 2, shoot number was not affected by mowing height when *C. esculentus* grew in competition from *L. perenne* (12.3 to 12.9 shoots) but was lower at the 2 cm mowing height than at the 5 cm mowing height in the absence of competition (47.2 versus 58.6 shoots) (Figure 5C).

Figure 7 near here.

3.3 Effect of clone

In experiment 1, clones Waregem2 and Desselgem produced, on average (over all mowing intervals, with and without competition), more tubers per pot than clone Oostkamp, 211 ± 25 and 185 ± 19 vs 144 ± 26 tubers respectively. There was also a main effect of clone on shoot number ($p < 0.05$). Waregem2 produced more shoots than Oostkamp (33.9 ± 2.88 versus 29.2 ± 2.42 shoots), the shoot number of Desselgem was not different ($p > 0.05$) from both clones (31.5 ± 2.41 shoots). For the three clones in experiment 1, Desselgem, Oostkamp, and Waregem2, a maximum reduction in fresh individual tuber weight of 95, 97, and 94% was achieved, respectively (Figure 8). These were achieved under the 2-weekly, weekly, and weekly mowing regimes, respectively. There was no clone effect on fresh tuber weight ($p > 0.05$). Clones only revealed differences in fresh individual tuber weight when they were not mown: Oostkamp produced heavier tubers than Desselgem and Waregem2 (Figure 8).

In experiment 2, for clones Oostkamp and Waregem2, the maximum reductions in tuber number were 93 and 86%, respectively, these were achieved under a weekly mowing regime (Figure 7A). Within the competition and no competition levels, clone Oostkamp produced 2.1 and 1.6 times less tubers than Waregem2 (Figure 7B). In the absence of competition, clones Oostkamp and Waregem2 produced 5.4 and 4.2 times more tubers, respectively, than with competition (Figure 7B). Clone Oostkamp produced 1.4 times heavier tubers than clone Waregem2 (0.237 ± 0.015 and 0.173 ± 0.011 g, respectively, averaged over all levels of competition, mowing regime, and mowing height). Both clones Oostkamp and Waregem2 produced a lower number of shoots with competition than without competition (12.9 and 12.4 versus 49.4 and 56.3 shoots for Oostkamp and Waregem2, respectively) (Figure 5A).

Figure 8 near here.

4 DISCUSSION

Our pot experiments are considered worst-case scenarios for controlling *C. esculentus* for several reasons. Firstly, the first cut was made at the 8-leaf stage of *C. esculentus*, 1 month after planting the *C. esculentus* tubers: this was done to allow a good establishment of the *L. perenne* seedlings. In both experiments, no tuber formation was observed at the start of the mowing regimes. Applying the first cut a few weeks earlier may strengthen the impact of regular mowing on the amount of newly produced tubers, as a result of the higher depletion of stored energy reserves at the first cut when shoots are cut close to their compensation point (when the rate of photosynthesis is equal to the rate of respiration). Schröder et al. (2021) advised the 2-5 leaf stage for an effective mechanical control. Secondly, the tubers were planted at a shallow depth of 4 cm, primary shoot production from these tubers uses less energy compared to shoots growing from deeper positioned tubers e.g. 15 cm and thus leaving more reserves for regrowth. Thirdly, *C. esculentus* monocultures and mixtures with *L. perenne* grew under greenhouse conditions. The warm climatic conditions are expected to be more favourable for the growth of the C4 species *C. esculentus* than for the C3 species *L. perenne.* Fourthly, in our experiments the grass sod was established together with *C. esculentus*. It is expected that the competitive ability of *L. perenne* would be stronger when *C. esculentus* was introduced in a pre-existing well-established grass sod. On the other hand, the use of pregerminated tubers in these experiments may have led to an overestimation of the effects as under natural conditions only a portion of the tubers germinate and dormant tubers are present. By repeating the mowing season-long, later germinating tubers can be affected as well.

Weekly and 2-weekly cutting within an 18-week period (i.e. 17 and 9 mowing passes, respectively) significantly reduced tuber production of *C. esculentus* grown with or without *L. perenne*, irrespective of experiment or year. However, the decrease was more pronounced in experiment 1 than in experiment 2 (97 versus 90% compared to the un-cut control without competition). For *C. esculentus* grown in competition with *L. perenne*, and under the same mowing intervals, reductions in tuber number of 98% (experiment 1) and 90% (experiment 2) were reached. Small differences in control levels between experimental years may be attributed to differential climatic conditions encountered during the growing season. Daily temperatures and global radiation were similar between years except for May during which the mean minimum daily temperature was 3°C (30%) higher in 2018 than in 2020 and for July during which mean maximum daily temperature and global radiation was 5°C and 19%

higher in 2018 than in 2020 (Figure 1). Warmer and sunnier growing conditions lead to faster and stronger (re)growth of the shoots after each cut, and hence, quicker and higher use of energy and nutrient reserves stored in their basal tubers (Li et al., 2000). Provided the regrowth is cut no later than the compensation point, fewer carbohydrate and nutrient reserves will be left for future resprouting capacity, shoot regrowth or tuberisation formation. Maximum reductions obtained in our study are in line with the results from Summerlin et al. (2000) who reached a control of tuber number up to 100% under a mowing interval with 1 or 3 cuts per week and a mowing height of 1.3 and 3.8 cm. Li et al. (2021) found much lower reductions in tuber number (63%) with weekly mowing. But in their experiment mowing height was set at 7.6 cm, leaving more green plant parts intact thus maintaining substantial photosynthetic capacity.

Mown *C. esculentus* stands produced significantly lighter tubers and lower tuber numbers than the uncut *C. esculentus* stands, irrespective of level of interspecific competition. In our experiments, the 8-, 4-, 2-, and weekly mowing intervals lead to a reduction in individual tuber weight of up to 37, 67, 96, and 97% respectively, compared to the uncut control. The production of lighter tubers facilitates future *C. esculentus* control in three ways. Firstly, although lighter tubers may be viable, regardless of their maturation stage, they will be less persistent as tuber longevity is positively correlated with tuber weight (Thullen and Keeley, 1975). Stoller and Wax (1973) found tuber half-lives of 4.4 and 5.8 months for newly formed tubers with an average dry weight of 75 mg/tuber buried in November at a depth of 10.2 and 20.3 cm, respectively. As the tubers produced under the weekly and 2-weekly mowing regimes were up to 4.7 times lighter (namely 16 and 26 mg, calculated by multiplying the mean fresh individual tuber weight of 20 and 30 mg by the mean dry matter content of 79 and 85% obtained under weekly and 2-weekly mowing, respectively), their half-lives are considered to be smaller than 4.4 months. Hence, it is expected that at least 70% of tubers produced under weekly and 2-weekly mowing regimes will lose their vitality long before outdoor soil temperatures in spring become suitable for germination (i.e. 12°C reached in April in Belgium, about 6 months after shoot senescence). Secondly, plants originating from lighter tubers are easier to control or deplete than their heavier counterparts (Thullen and Keeley, 1975) as lighter tubers have lower carbohydrate reserves (Stoller et al., 1972). Thirdly, shoots from light tubers are less capable of emerging than shoots from heavy tubers as shown by Stoller et al. (1972) and Stoller and Wax (1973).

Strategies with repeated mowing at 2 or 5 cm, in absence of a competitor, were not able to fully prevent tuber formation and decrease the tuber bank, irrespective of mowing interval. Hence, mowing without competition is not sufficient. Competition with other plant species is crucial as the production of tubers is density-dependent and likely reduced when growing with other species (Follak et al., 2016). More importantly, competition for light is crucial as tuber production can be reduced up to 100% by light competing species (Keeley and Thullen, 1978; Lotz et al., 1991; Santos et al., 1997b; Bohren and Wirth, 2015). Indeed, over all mowing regimes in both our experiments, reductions in tuber number up to 86% were reached in the presence of *L. perenne*. In the uncut control treatments, reductions in tuber number up to 82% (141 vs. 751 tubers averaged over the clones with and without competition respectively) were achieved by installing *L. perenne* as a competitor, confirming the results found by the aforementioned authors. As aboveground defoliation alone won't suffice to reduce the number of tubers in the bud bank of grassy areas, these grasslands should ideally contain highly competitive species that are able to withstand regular mowing at low heights, such as *L. perenne*. Control levels obtained by a regime without mowing but with *L. perenne* competition was equivalent to a 2-weekly (experiment 2) and 4-weekly (experiment 1) mowing interval of *C. esculentus* grown without competition.

When *C. esculentus* grew in the presence of *L. perenne*, mowing had no significant effect on shoot number, irrespective of mowing height or mowing interval. When grown in absence of this competitor, a significant reduction in shoot number was achieved by mowing weekly (experiment 2) or 2-weekly (experiment 1). Seemingly, the presence of a competitor (*L. perenne*) is more effective in reducing shoot number than narrowing the mowing interval (Figure 3). Shoot number was up to 3 times lower in unmown treatments with competition than in weekly mown treatments without competition, indeed. These observations are in line with Kolberg et al. (2018) who found that reductions in shoot number of *Elymus repens* L. (quackgrass) were more pronounced when grown in competition with *Trifolium repens* L. (white clover) than after regular shoot defoliation (each time *E. repens* reached two leaves). Most likely, *C. esculentus* grown in competition from *L. perenne* attempts to overgrow *L. perenne* by preferential allocation of limited carbohydrate and nutrient reserves to the growth of a few existing main shoots rather than to new shoot formation (through formation of new rhizomes that form basal bulbs on their tips). The lower shoot number reductions obtained for *C. esculentus* plants under repeated defoliation, may likely be explained by preferential allocation of carbohydrates and nutrients to shoot formation in their attempt to quickly occupy more space and maximize photosynthetically active biomass staying below the cutting height. However, reductions in shoot number were more pronounced for *C. esculentus* (up to 46% decrease) than for *E. repens* (up to 9% increase) in the study of Kolberg et al.

(2018). Unlike *E. repens*, *C. esculentus* is not able to tiller in response to mowing indeed. Shoot number was not affected by mowing height unless under a weekly mowing interval at which shoot number was 4.4 times lower at 2 cm height than at 5 cm height. In treatments without competition from *L. perenne*, reductions in shoot number go hand in hand with reductions in tuber number. This is no surprise given the strong positive correlation between both parameters found by De Cauwer et al. (2017) and De Ryck et al. (2023) in pure stands of *C. esculentus*.

To conclude, we found that the most intense defoliation strategy (weekly mowing at 2 cm) was the most effective (up to 98% reduction in tuber number) in reducing reproductive potential of *C. esculentus*. High cutting frequency with a low recovery time between cuttings and low cutting height makes it more difficult for plants to compensate for the loss of photosynthetically active biomass and hence to allocate carbohydrate reserves to belowground biomass accumulation. However, given that reductions in tuber number obtained under weekly and 2-weekly mowing regimes did not significantly differ and that weekly mowing is impractical to apply, mowing every 2 weeks is deemed most appropriate and was found to be the critical mowing interval. The lower the mowing height (mowing at 2 vs 5 cm), the better *C. esculentus* is controlled, with tuber numbers up to 32% lower and 5-65% lighter under a 2 cm mowing height versus a 5 cm mowing height. Competition plays an important role in aiding to lower the amount of newly produced tubers, even without mowing. In grassy field margins, an optimal mowing regime should consist of a 2-weekly mowing interval and a 2 cm mowing height, regardless of the clone that is present. This stringent mowing regime did not fully inhibit tuber formation but tubers formed were light in weight and therefore too short-lived to be capable of sprouting in the next spring. Hence, 2-weekly mowing at 2 cm is highly advisable for containing or reducing *C. esculentus* patches in herbaceous and grassy field margins in order to reduce species ingrowth into the adjacent crop.

AUTHOR'S CONTRIBUTION

Sander De Ryck: Conceptualization; methodology (equal); investigation; formal analysis (lead); writing - original draft; writing - review and editing. **Dirk Reheul**: Writing - review and editing. **Benny De Cauwer**: Conceptualization (lead); methodology (equal); writing - review and editing (lead).

CONFLICT OF INTEREST

There are no conflicts of interest.

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Figure legends

FIGURE 1 Maximum and minimum daily temperature (°C), cutting times for weekly, 2-weekly, 4-weekly and 8-weekly mowing, and daily global radiation (J cm^{-2}) during the experimental period in 2018 (A, experiment1) and 2020 (B, experiment 2).

FIGURE 2 Tuber number (mean ± SE) for all factorial combinations of mowing interval (uncut control, 8-weekly, 4-weekly, 2-weekly, weekly) and *L. perenne* competition level (no competition, competition) in experiment 1 (n = 24) (A) and experiment 2 (n = 16) (B). The Tukey-HSD test was used to check for significant differences ($p < 0.05$).

FIGURE 3 Shoot number (mean ± SE) for all factorial combinations of mowing interval (uncut control, 8-weekly, 4-weekly, 2-weekly, weekly) and *L. perenne* competition level (no competition, competition) in experiment 1 (n = 24) (A) and experiment 2 (n = 16) (B). The Tukey-HSD test was used to check for significant differences ($p < 0.05$).

FIGURE 4 Fresh tuber weight (mean ± SE) for all factorial combinations of mowing interval (uncut control, 8-weekly, 4-weekly, 2-weekly, weekly) and *L. perenne* competition level (no competition, competition) in experiment 1 (n = 24) (A) and experiment 2 (n = 16) (B). The Tukey-HSD test was used to check for significant differences ($p < 0.05$).

FIGURE 5 Shoot number (mean ± SE) for all factorial combinations of *L. perenne* competition level (no competition, competition) and clone (Oostkamp, Waregem2) (n = 40) (A), mowing interval (uncut control, 8-weekly, 4-weekly, 2-weekly, weekly) and mowing height (2 cm, 5 cm) (n = 16) (B), and *L. perenne* competition level and mowing height (n = 40) (C) in experiment 2. The Tukey-HSD test was used to check for significant differences ($p < 0.05$).

FIGURE 6 Fresh individual tuber weight (mean ± SE, n = 16) for all factorial combinations of mowing interval (uncut control, 8-weekly, 4-weekly, 2-weekly, weekly) and mowing height (2 cm, 5 cm) combinations in experiment 2. The Tukey-HSD test was used to check for significant differences ($p < 0.05$).

FIGURE 7 Tuber number (mean ± SE) for the factorial combinations of mowing interval (uncut control, 8-weekly, 4-weekly, 2-weekly, weekly) and clone (Oostkamp, Waregem2) (n

= 16) (A), *L. perenne* competition level (no competition, competition) and clone (n = 40) (B), and competition level and mowing height (2 cm, 5 cm) (n = 40) (C) in experiment 2. The Tukey-HSD test was used to check for significant differences ($p < 0.05$).

FIGURE 8 Fresh individual tuber weight (mean ± SE, n = 16) for all factorial combinations of mowing interval (uncut control, 8-weekly, 4-weekly, 2-weekly, weekly) and clone (Desselgem, Oostkamp, Waregem2) in experiment 1. The Tukey-HSD test was used to check for significant differences ($p < 0.05$).

TABLE 1 The significance of the main effects and two-, three-, and four-factor interactions of the full model for all the measured and calculated variables in experiment 1.

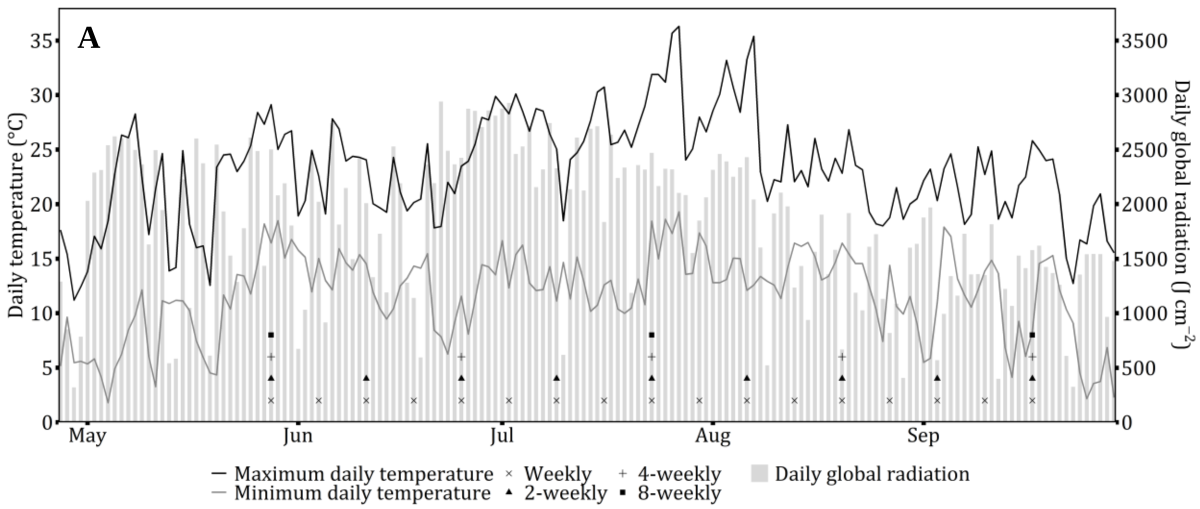
ANOVA-model	Tuber number	Fresh tuber weight	Fresh individual tuber weight	Shoot number
Mowing interval	***	***	***	***
Competition	***	***	**	***
Clone	**	NS	NS	*
Tuber size	NS	NS	NS	NS
Block	NS	NS	NS	NS
Mowing interval:Competition	***	***	NS	***
Mowing interval:Clone	NS	NS	*	NS
Competition:Clone	NS	NS	NS	NS
Mowing interval:Tuber size	NS	NS	NS	NS
Competition:Tuber size	NS	NS	NS	NS
Clone:Tuber size	NS	NS	NS	NS
Mowing interval:Competition:Clone	NS	NS	NS	NS
Mowing interval:Competition:Tuber size	NS	NS	NS	NS
Mowing interval:Clone:Tuber size	NS	NS	NS	NS
Competition:Clone:Tuber size	NS	NS	NS	NS
Mowing interval:Competition:Clone:Tuber size	NS	NS	NS	NS

Significance: NS (not significant), * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$)

TABLE 2 The significance of the main effects and two-, three-, and four-factor interactions of the full model for all the measured and calculated variables in experiment 2.

ANOVA-model	Tuber number	Fresh tuber weight	Fresh individual tuber weight	Shoot number
Mowing interval	***	***	***	***
Competition	***	***	NS	***
Clone	***	NS	***	*
Height	***	NS	***	***
Block	NS	NS	NS	NS
Mowing interval:Competition	***	***	NS	**
Mowing interval:Clone	*	NS	NS	NS
Competition:Clone	**	NS	NS	*
Mowing interval:Height	NS	NS	**	***
Competition:Height	***	NS	NS	**
Clone:Height	NS	NS	NS	NS
Mowing interval:Competition:Clone	NS	NS	NS	NS
Mowing interval:Competition:Height	NS	NS	NS	NS
Mowing interval:Clone:Height	NS	NS	NS	NS
Competition:Clone:Height	NS	NS	NS	NS
Mowing interval:Competition:Clone:Height	NS	NS	NS	NS

Significance: NS (not significant), * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$)


A
Daily temperature (°C)
Daily global radiation (J cm^{-2})
May
Jun
Jul
Aug
Sep
Maximum daily temperature
Minimum daily temperature
Weekly
2-weekly
4-weekly
8-weekly
Daily global radiation

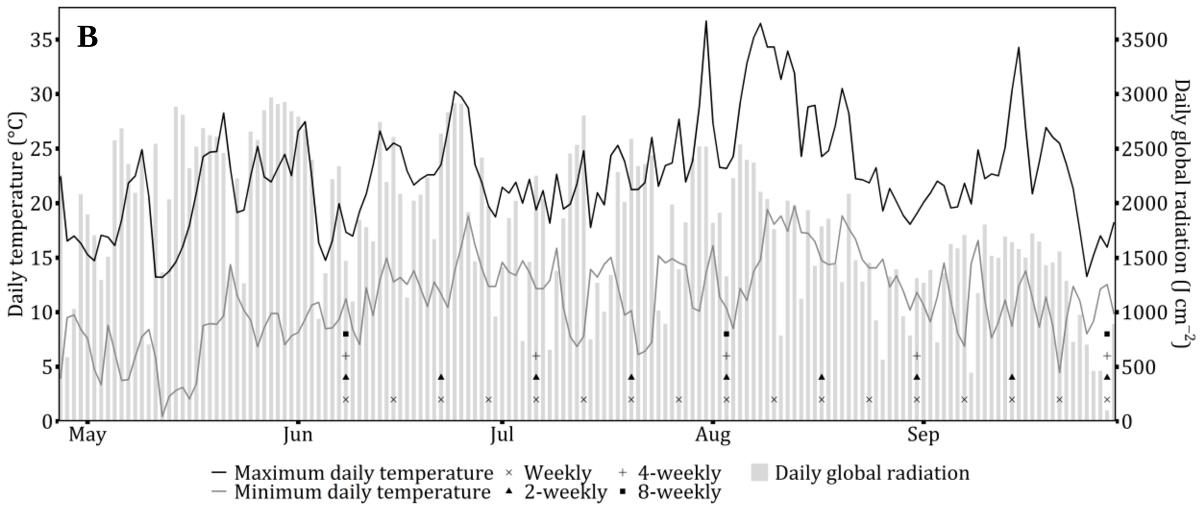

B
Daily temperature (°C)
Daily global radiation (J cm^{-2})
May
Jun
Jul
Aug
Sep
Maximum daily temperature
Minimum daily temperature
Weekly
2-weekly
4-weekly
8-weekly
Daily global radiation

FIGURE 1

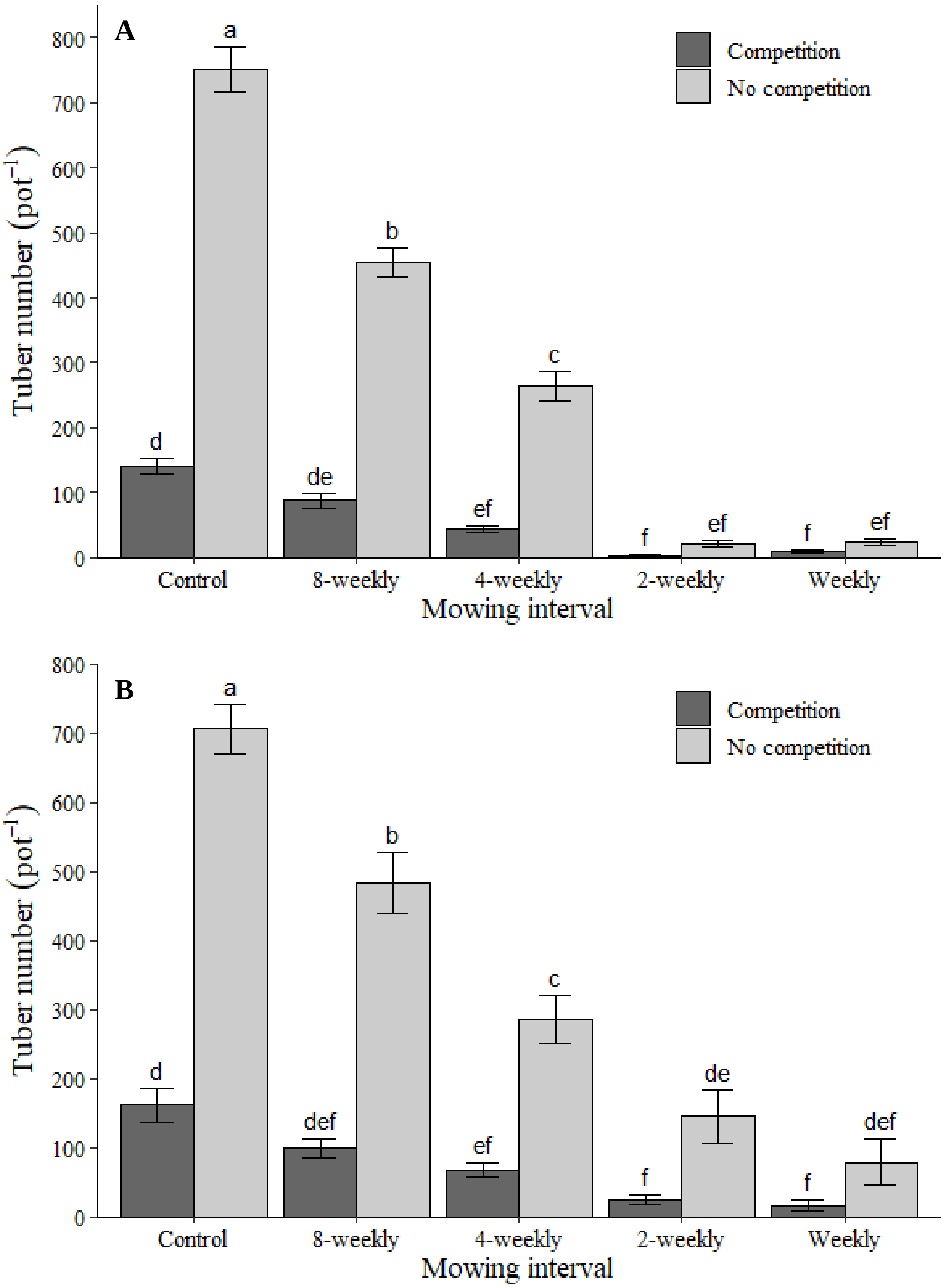

A
B
Tuber number (pot^{-1})
Mowing interval
Competition
No competition
Control
8-weekly
4-weekly
2-weekly
Weekly
0
100
200
300
400
500
600
700
800
a
b
c
d
de
def
ef
f

FIGURE 2

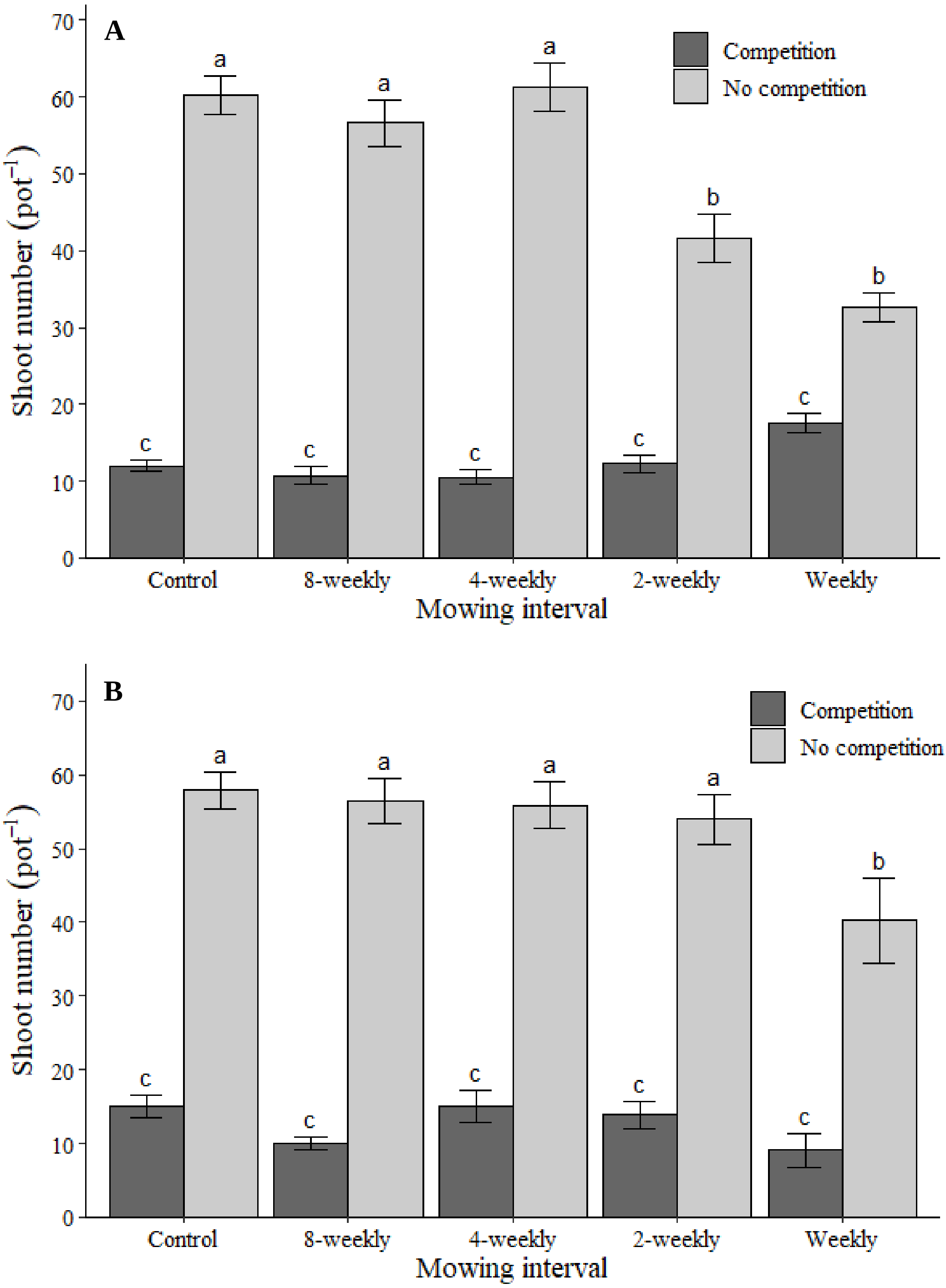

A
B
Competition
No competition
Shoot number (pot^{-1})
Mowing interval
Control
8-weekly
4-weekly
2-weekly
Weekly
0
10
20
30
40
50
60
70
a
b
c

FIGURE 3

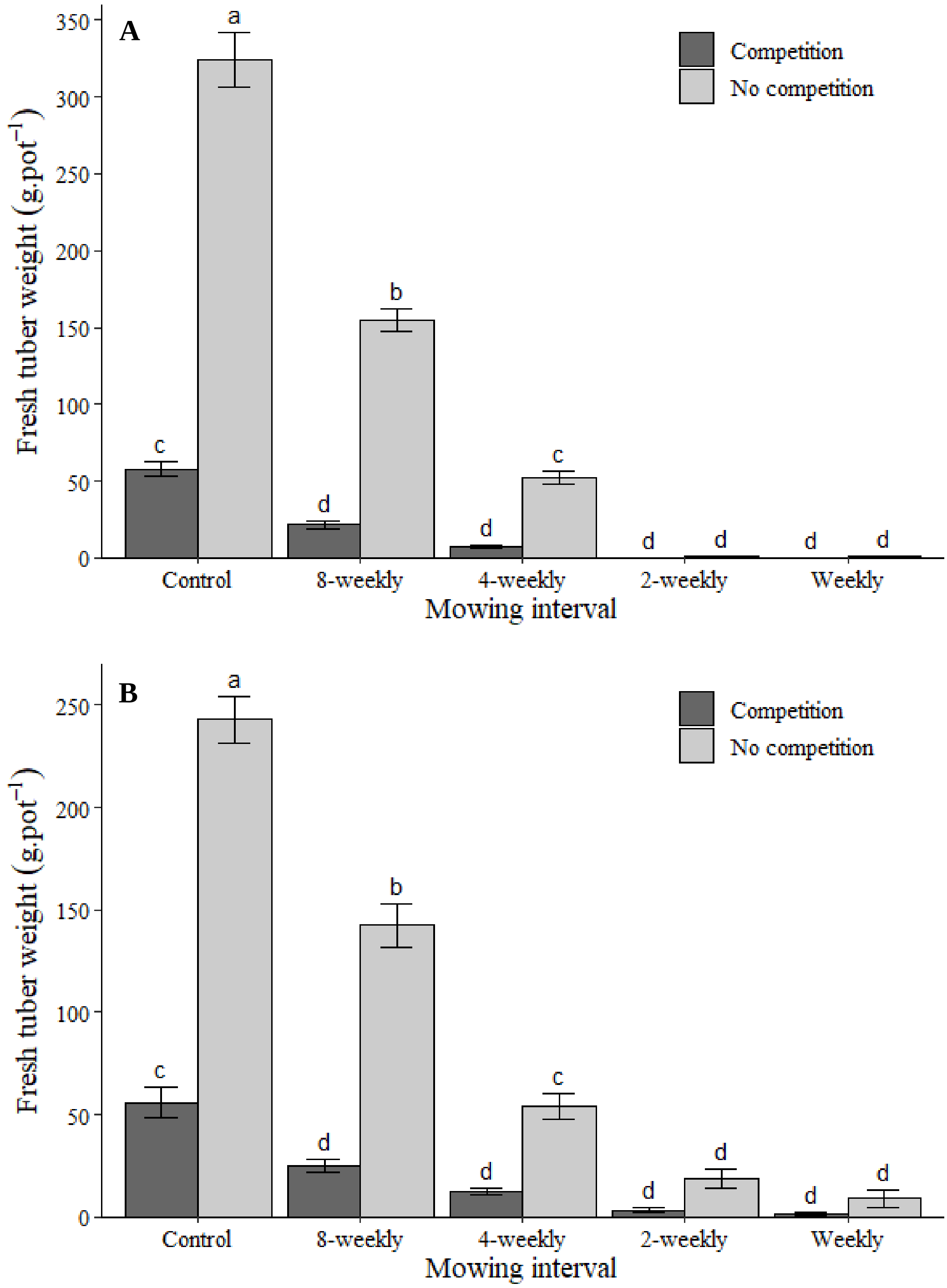

A
B
Competition
No competition
Fresh tuber weight (g.pot^{-1})
0
50
100
150
200
250
300
350
a
b
c
d
Control
8-weekly
4-weekly
2-weekly
Weekly
Mowing interval

FIGURE 4

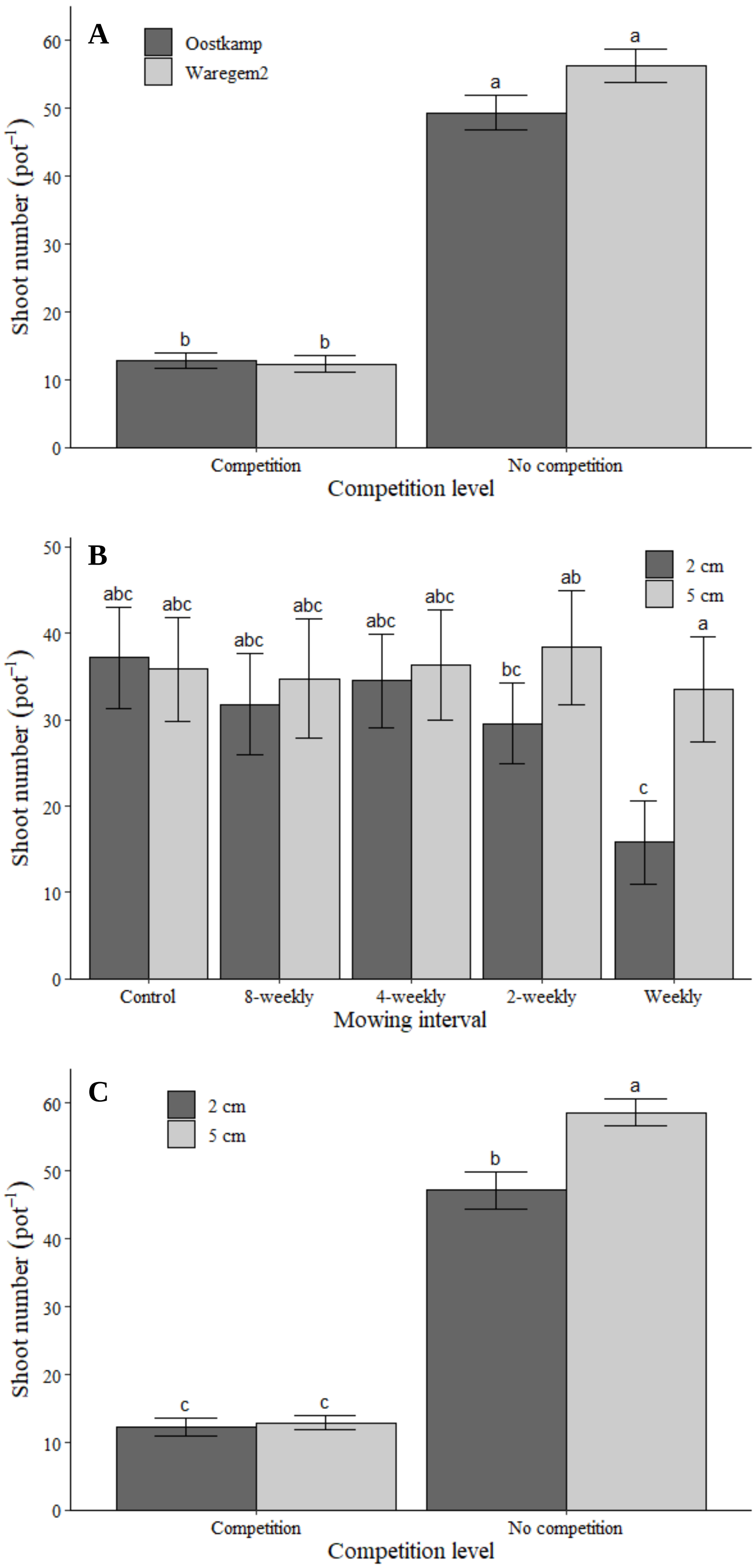
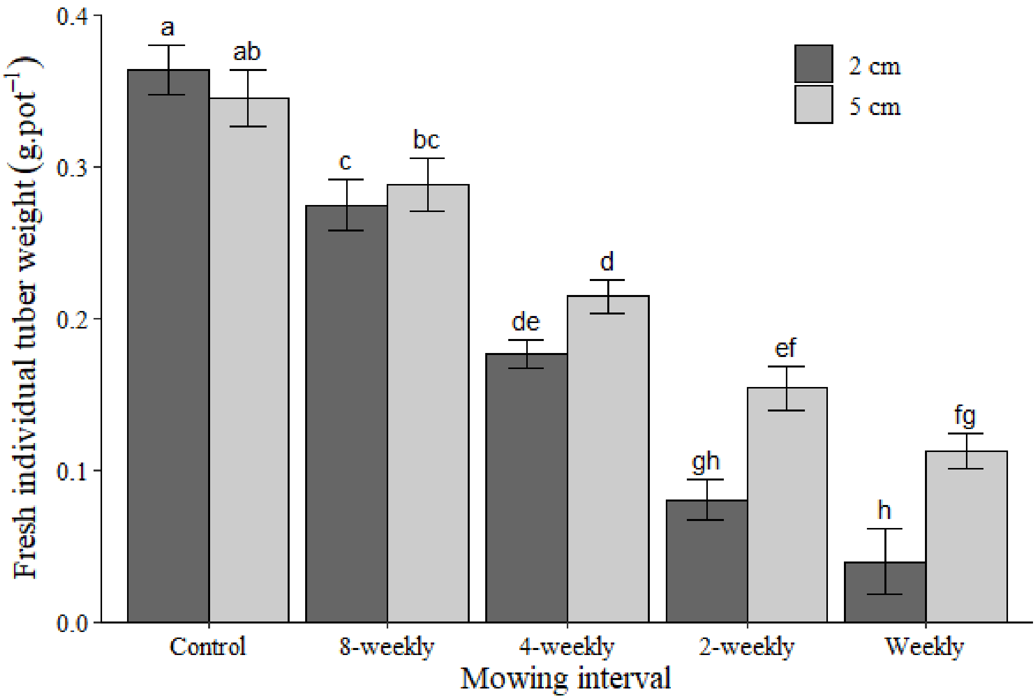

A
Oostkamp
Waregem2
Shoot number (pot^{-1})
Competition
No competition
Competition level
B
2 cm
5 cm
Shoot number (pot^{-1})
Control
8-weekly
4-weekly
2-weekly
Weekly
Mowing interval
C
2 cm
5 cm
Shoot number (pot^{-1})
Competition
No competition
Competition level

FIGURE 5



Fresh individual tuber weight (g.pot^{-1})
0.4
0.3
0.2
0.1
0.0
a
ab
c
bc
de
d
gh
ef
h
fg
2 cm
5 cm
Control
8-weekly
4-weekly
2-weekly
Weekly
Mowing interval

FIGURE 6

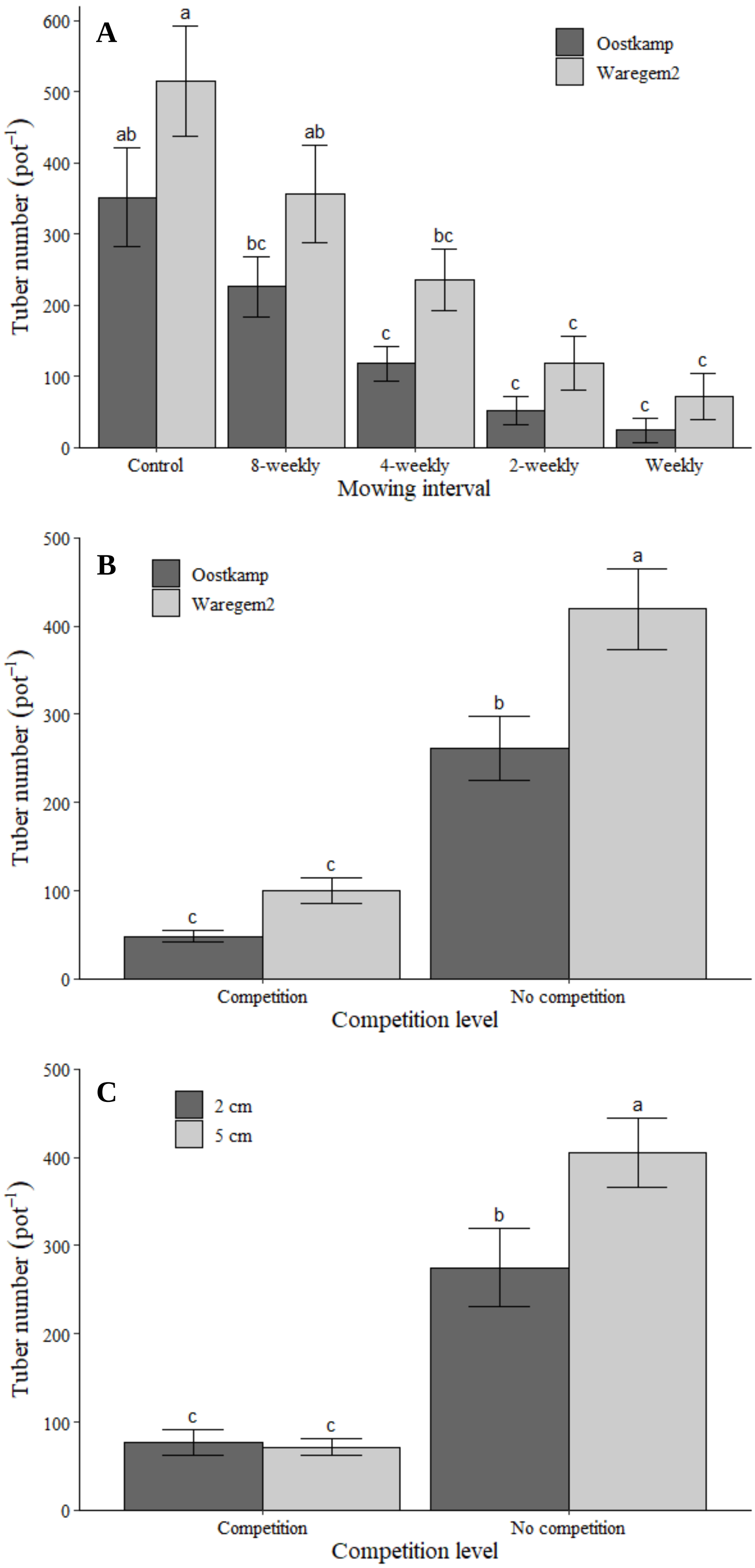
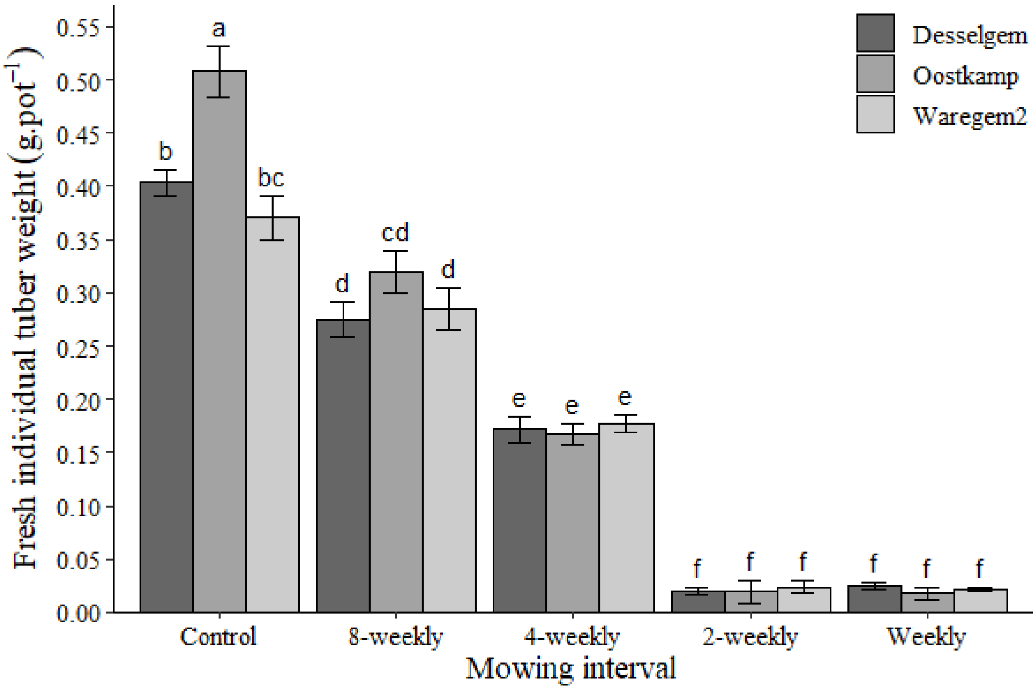

A
Oostkamp
Waregem2
Tuber number (pot⁻¹)
600
500
400
300
200
100
0
a
ab
ab
bc
bc
c
c
c
c
c
Control
8-weekly
4-weekly
2-weekly
Weekly
Mowing interval
B
Oostkamp
Waregem2
Tuber number (pot⁻¹)
500
400
300
200
100
0
a
b
c
c
Competition
No competition
Competition level
C
2 cm
5 cm
Tuber number (pot⁻¹)
500
400
300
200
100
0
a
b
c
c
Competition
No competition
Competition level

FIGURE 7



Fresh individual tuber weight (g.pot^{-1})
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
a
b
bc
cd
d
d
e
e
e
f
f
f
f
f
f
Desselgem
Oostkamp
Waregem2
Control
8-weekly
4-weekly
2-weekly
Weekly
Mowing interval

FIGURE 8