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Drought conditions, tillage regime and soil phosphorous modulate the incidence of weeds, pests and pathogens in arable crops

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Drought events are expected to become increasingly frequent, with potentially severe aftermaths on agriculture through direct and indirect effects on crops. It is thus necessary to understand how management practices can mitigate the impacts of droughts on yields, harmful organisms and ecosystem service providers in different soil contexts. Soil disturbance reduction is often suggested as one such practice.

In this study, we investigated the effects of drought (50% reduction in natural precipitation), tillage regime (conservation vs. conventional tillage), and the pivotal soil nutrient phosphorous on crop yield, as well as on the control of weeds, pests, and pathogens. We set our manipulative experiment in 18 arable fields in Northern Italy, and drought conditions were simulated with rainout shelters.

Drought had a negative effect on yields and increased the biomass and species richness of weeds. Conservation tillage had lower crop disease incidence but higher weed biomass than conventional tillage. Drought and conventional tillage both reduced the number of synergies between the different ecosystem services indicators. Soil phosphorus increased weed biomass, but decreased disease incidence in soybean. Arthropod pests and predators were not significantly affected by any of the tested variables.

Against the predictions, the effects of conservation tillage on drought mitigation and ecosystem services were mixed, indicating that complex combinations of multiple interventions will be required to reduce the negative effects of drought, weeds and pests under a changing climate.

Keywords Biological control, Climate change, Conservation agriculture, Ecosystem services, No-till, Seed decay

Climate change is one of the greatest environmental challenges of our time with far-reaching consequences on many human activities, including agriculture[1]. Meteorological drought conditions, defined as precipitation deficits, are expected to become increasingly common[2], which might negatively impact agriculture affecting crop yields[3]. Meteorological drought, in fact, is linked with agricultural drought, defined as a deficit in soil moisture and, therefore, in soil water availability to plants[4]. Increasing temperatures—while generally accelerating crop development and growth[5]—also lead to higher evapotranspiration and eventually water stress in plants, severely limiting crop productivity[6]. Climate-change-induced drought can also indirectly impact crop yields by generally favouring organisms noxious to the crop itself; these may include weeds, animal pests and pathogens. Given the wildly different biology and general ecology of these 3 groups, sustainable agroecological strategies to control them – either through natural enemies (biological control as an ecosystem service) or other means – need to focus on different aspects of the agroecosystem[7]. The situation is complicated by the fact that the same management action can differentially affect different ecosystem services, leading to trade-offs between them[8]. Consequently, there is a great interest in understanding how to minimize such trade-offs and exploit

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the generally rarer ecosystem service synergies—commonly defined, respectively, as negative and positive associations between two or more services in response to a given variable[9,10].

Among harmful organisms, weeds deserve particular attention as they represent one of the most important biotic factors limiting crop yields worldwide[11]. Many weed species with traits related to efficient water exploitation are expected to expand their ranges and increase in abundance under drier conditions[12]. One of the key advantages of weeds over crops is their diversity, both at the genetic and community level, which allows them to exploit a variety of niches and persist through environmental changes and stresses, including attempts at weed control[13]. In contrast with weed biomass, however, weed diversity can also have positive effects on the functioning of agroecosystems, including support to beneficial arthropods and other wildlife[14]. Additionally, weeds do not only compete against the crop but also against each other, with some weed species potentially limiting dominant species and mitigating their negative effects[15]. Seeds are a key life stage through which drought could exert its effect on weeds. Seed germinability is in fact known to respond dramatically to drought-induced changes in the physical and biological features of soil[16,17]. Additionally, soil microorganisms can degrade buried seeds[18] and therefore perform biological weed control[19], an attractive alternative to herbicides and their deleterious environmental effects[20]. The effects of climate change on soil microbiomes and the associated ecosystem services are understudied[21], but there is evidence that arid conditions can negatively impact soil microbe abundance and diversity[22], potentially eroding their ability to degrade seeds – although physiological and evolutionary adaptation mechanisms might maintain soil microbial functions in certain conditions[23].

Other important yield limiting factors for crops worldwide are invertebrate pests and pathogens, both of which are projected to be affected by climate change as well[24]. Just like weeds, many pest species could shift their ranges and generally benefit from climate change, increasing in numbers[25] – although in some cases they might also suffer from negative impacts of more extreme climatic conditions and events[26]. Additionally, plants suffering from water stress in drought conditions might have reduced chemical defenses or increased nutrient concentration, becoming a higher-quality resource for herbivores as per the plant stress hypothesis[27,28]. Natural enemies such as predators or parasitoids are often seen as beneficial organisms, because they can act as an environmentally friendly tool for the control of pests[29]. Climate change effects on these biocontrol agents are expected to be complex, with the repercussions on pest control being equally difficult to predict[30]. As for plant pathogens, climate change could not only alter their biology and range, but also impact the physiology of host plants through drought and other stresses, potentially making plants more vulnerable to infection[31].

Soil features and management play a pivotal role in influencing crop productivity and sustainability. Conservation tillage regimes that reduce soil disturbance improve soil physical features[32] and favor a series of beneficial organisms living in the soil such as natural enemies of pests and weeds[33,34] and microorganisms linked with soil fertility[35], which in turn can influence the related ecosystem services[34,36,37]. Conservation tillage has also been proposed as a way to reduce carbon emissions and mitigate climate change[38]. Even more crucially in the context of this paper, conservation tillage has been proposed as a way to reduce the deleterious effects of drought on crops, either directly by reducing soil moisture loss[39] or indirectly by favoring beneficial organisms[40]. Conservation tillage, however, also presents significant drawbacks, including influencing weed communities[41] often resulting in a higher incidence of weeds in the fields[42]. A careful choice of soil management strategies might thus prove pivotal in offsetting some of the most harmful effects that climate change has on agriculture either through negative impacts on beneficial organisms or positive impacts on weeds, pests and pathogens. Another factor that pertains to soil and climate change is nutrient availability. The ability of plants to exploit soil nutrients can be significantly hampered by drought, as it has been shown for the important limiting macronutrient phosphorous[43]. It is well known that phosphorus has a pivotal role in influencing crop yield[44] and modulating multiple ecosystem services[45–47]. It is also considered one of the best indicators of soil fertility [48]. The ability of plants to uptake soil phosphorous has in fact been shown to be particularly sensitive to negative effects caused by drought when compared to other limiting macronutrients such as nitrogen[49,50]. It follows that the soil phosphorous concentration necessary for crops to reach a given yield may vary depending on the severity of drought conditions.

The aim of this study was to investigate the combined effects of climate-change-induced drought (simulated through rainout shelters), tillage regime and soil phosphorous availability (detected as a natural gradient in the experimental fields) on the yields of soybean (*Glycine max* (L.)) and wheat (*Triticum aestivum* L.), and on important parameters linked with the natural control of weeds, pests and pathogens; the latter included weed biomass production, weed diversity, weed seed decay, herbivore arthropod abundance, predatory arthropod abundance and soybean leaf disease incidence. The study took place in 9 field pairs (conventional vs. conservation tillage) in the Friuli plain of Northern Italy. We hypothesized that conservation tillage and natural phosphorous availability would mitigate the deleterious effects of drought on ecosystem services and yield, and that tillage and drought would also influence the number and identity of trade-offs and synergies among ecosystem services. Specifically, we expected conservation tillage and normal rainfall to increase synergies and reduce trade-offs, as stressful factors such as conventional tillage and excessive fertilization have been found to cause an opposite effect[34]. Given the high influence that weeds have on crops[11], it was reasonable to assume that weed control and crop yield would be frequently correlated, while weed control and arthropod predator abundance was considered a likely trade-off due to the positive effects that weeds can have on natural enemy populations[14].

Methods

Study area and experimental design

Experiments were carried out between 2018 and 2019 across 9 field pairs in the lowland area of the Friuli Venezia Giulia Region (NE Italy), within an agricultural landscape (c. 615 km^2) characterized by temperate climate (mean annual precipitation of c. 1300 mm; mean annual temperature of 13 °C). Each pair included one conventional tillage field and one conservation tillage field (Fig. 1). In our case, all techniques characterized by non-inversion of soil for at least 8 to a maximum of 18 years were considered as "conservation tillage". The distance between fields in a pair was less than 300 m except for one in which it was 900 m (Supplementary Table S1). The minimum distance between different pairs was 450 m, the maximum distance was 39 km; the specific coordinates of each experimental field can be found in Supplementary Table S1. In all fields, soybean was sown in May 2018 and harvested in October 2018, while wheat was sown in November 2018 and harvested in June 2019.

Soil characterization

Topsoil cores of 40 cm depth were collected in each field at the end of June 2018 and analyzed for content of carbon and phosphorous and for texture (i.e. silt, clay and sand content) (Supplementary Table S2). Soil phosphorus was quantified using the Olsen method[51]. A gradient in natural soil phosphorous availability detected across the selected experimental fields allowed to test the interactive effect of tillage regime and drought across varying soil fertility conditions. Phosphorous was not significantly linked with tillage regime in our data; additionally, phosphorous was only measured in normal rainfed conditions, as phosphorous soil levels are mainly dependent on artificial fertilization on the short term, while it is phosphorous availability to plants that is influenced by drought[49,50].

Drought treatment

In each field, we defined a 20 × 60 m cultivated strip at the field margin in which agrochemicals (including fertilizers) were not used. Roughly at the center of this strip, we selected a 4 × 4 m drought treatment plot and an equally sized rainfed control plot (Fig. 1). The drought and the rainfed plot were placed at around 1 m from each other, to ensure homogeneity of conditions. Half of the area of each drought and rainfed plot was normally sown with the crop, while the other half was left unsown. The sown half represented a realistic situation for measuring crop yield production under the different treatments, while the unsown half was used to gather more data on weed diversity and growth. The latter is a less realistic scenario as weeds experienced increased growth, being free of competition with crops, but the method allowed us to gather more detailed data on weed community responses to drought, tillage and phosphorous that would be valuable for understanding baseline weed ecology.

The drought treatment was implemented using 4 × 4 m removable rainout shelters[52]. The roofs of the shelters were covered with 18 polycarbonate gutters (11 cm wide, 400 cm long and 3 cm deep) evenly distributed in order to exclude about 50% of the precipitations, with the space between one gutter and the next being roughly 11 cm wide. The shelters were 170 cm high on one side and 150 cm high on the opposite side, water was collected in a

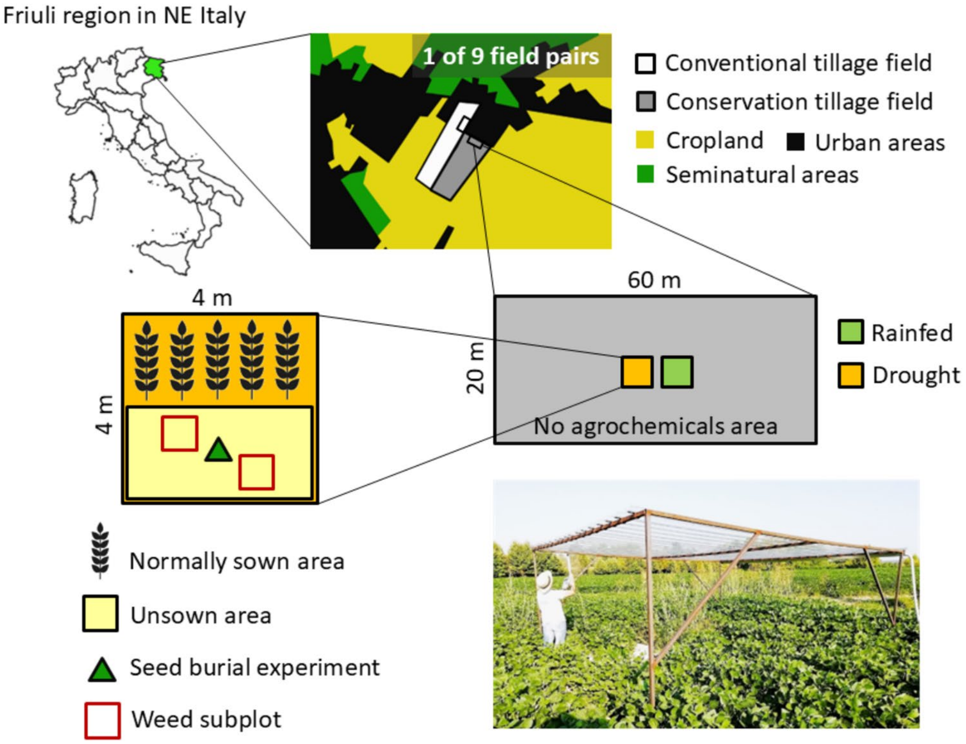

Fig. 1. Experimental design with a picture showing a drought treatment plot under a rainout shelter. Each of the 9 field pairs included a conservation tillage field and a conventional tillage field; in each field, we selected a 20 × 60 m area where no agrochemicals were applied; in each of these areas, we selected a drought treatment plot and a control rainfed plot; in each plot, we had a normally sown half (for yield, disease, predators and pests) and an unsown half (for weeds); in the unsown half, se selected two subplots for the study of weeds, and we performed the seed burial experiment.

common gutter at the back of the shelter and then released on field at about 5 m from the plot through a plastic tube. Shelters were placed in the field one week after soybean sowing and temporarily removed in between soybean harvesting and wheat sowing. It is important to note that the exclusion of 50% of precipitations does not mean that shelters are able to simulate a 50% drought, as underground and air humidity can percolate from surrounding areas, which is inevitable under realistic field conditions; in spite of these known limitations, rainout shelters remain a standard and widespread method for the study of drought effects on vegetation, due to their versatility and ease of use[53]. We had a total of 36 experimental plots, 9 for each tillage/drought combination.

To better quantify the effect of the rainout shelters on soil moisture, from May to October 2018 (the soybean period) we monitored three field couples using ECH$_2$O EC-5 soil humidity probes and ICT Em5b data loggers (Supplementary Table S1). In each drought and rainfed plot, two probes were buried at 20 cm of depth and data loggers registered humidity levels every 30 min from the placement to the removal of the shelters. Mean volumetric water contents per month are reported in Supplementary Table S3.

Crop yield

At soybean and wheat harvest phase, we harvested 1 m^2 of each crop in each experimental plot using a plastic quadrat as a reference. We then dried the seeds (70 °C for 72 h) and measured their dry weight, which was used as a proxy for yield. In one of the rainfed plots of conservation tillage, wheat could not be harvested due to storm damage.

Herbivores, predators and pathogen survey

Two visual surveys were carried out on soybean in the first half of July and in the first half of September of 2018. During each survey, 20 soybean plants per plot were randomly selected, and all leaves of each plant were carefully checked. We recorded the number of potentially damaging herbivore arthropods and potentially beneficial predatory arthropods in each plot. Additionally, during these surveys we recorded the incidence of pathogens, measured as the percentage of surveyed plants that showed signs of infection. Herbivores, predators and pathogens were not identified to the species level, although herbivores and predators were categorized into their main families/orders. These surveys could not be carried out on wheat due to entomological operator unavailability.

Buried seed decay

We selected 3 weed species, representing different seed shapes and sizes, to test the seed decay capabilities of soil physical features and soil microbes under the different treatments. The species were *Abutilon theophrasti* Medicus, *Amaranthus retroflexus* L. and *Digitaria sanguinalis* (L.) Scop. Mature seeds of these species were hand-collected at the experimental farm of the University of Padova "Lucio Toniolo" (45°20′53.99″N, 11°57′5.46″E). The seeds were air-dried, mechanically cleaned, and stored at 4 °C until use. For each species, metal wire mesh bags (mesh size: 1 mm^2) were prepared, each with 50 seeds sealed inside. This prevented invertebrates from preying on the seeds and confounding the effects of seed decay; the bags were flexible enough to allow the contact between soil and seeds[54]. In each drought and rainfed plot, we buried 4 seed bags per species. Due to organizational limitations, we could perform this experiment in only 8 of the 9 field pairs, resulting in a total of 128 buried seed bags per plant species. Bags were buried side by side at the depth of 15 cm, in a 60 × 25 cm hole, roughly at the center of the unsown half of the plot. Seeds remained underground from December 2018 to June 2019 (6 months). In one of the field pairs, data was lost due to external interference.

The recovered seeds initially underwent a crush test[55], during which crushed seeds were classified as degraded. The remaining seeds were then tested for germinability by putting them in a growth chamber, i.e. seeds were placed in Petri dishes with filter paper bedding and 2 mL of distilled water, at 15/25 °C with a 12/12 h light/dark photoperiod[54]. Petri dishes were sealed with Parafilm, and more water was added when needed. Every 2 days, seeds were checked and the ones with a visible root were considered germinated and removed. When no new germinations were observed for a period of 10 days, seeds were moved in cold storage at 4 °C for 3 weeks and then moved back in the growth chamber and the process repeated, to interrupt a possible state of quiescence. After another 10 days since the last observed germination, the remaining seeds were cut in half, individually stored into Eppendorf vials with 1% tetrazolium and left at 30 °C in the dark for 24 h. At the end of the process, seeds were considered still vital if their interior was colored red. The proportion of the number of degraded and non-vital seeds over the total number of seeds was used as the measure of seed decay.

Weed diversity and biomass

Weed diversity was evaluated in two 1 × 1 m subplots placed in the unsown half of each drought and rainfed plot, at the distance of at least 70 cm from the border of the drought/rainfed plot. Due to botanical operator availability, surveys were carried out in February and April of 2019, after shelters had been in place exerting their action through all the soybean period, but before the sowing of wheat. Plant species were identified during the field survey, resulting in a measure of weed species richness in each subplot. At the time of wheat harvest in June 2019, all weed biomass was gathered from the subplots, dried for 48 h at 65 °C and then weighed. In one of the rainfed plots of conservation tillage, weed biomass could not be gathered due to external interference.

Data analysis: effects of drought, tillage and soil phosphorous

We used linear mixed effects models (LMMs) to evaluate the effect of drought treatment, tillage regime and soil phosphorus content on the yield of soybean and wheat as well as on weed seed decay, weed biomass and weed diversity, respectively. We started by testing the 3-way interaction between drought, tillage and phosphorous (which henceforth may be collectively indicated as "explanatory variables") and removing non-significant interactions to avoid overfitting and to correctly interpret the main effects. For predator abundance, herbivore abundance and disease incidence, we ran a Poisson, negative binomial and binomial generalized linear mixed effects model (GLMM) respectively. The choice of LMMs rather than GLMMs for seed decay and weed species richness, and model choice in general, was informed by the validation plots. Weed seed decay was square-root transformed in order to meet model assumptions. Models were calculated using package *lme4*[56] and validation plots were generated with package *DHARMa*[57] in R v3.6.2[58].

In the models for soybean and wheat yield, we used field pair ID and field ID as nested random factors. For most of the other models we used pair ID, field ID and plot ID as nested random factors to account for multiple measures in each plot – i.e. predators, herbivores and pathogens were surveyed twice per plot, weed biomass was collected in two subplots in each plot and weed seed decay was tested with multiple seed bags (4 for each of the 3 species) per plot. For weed species richness, we also used subplot ID as a nested random factor along with the previously mentioned ones, as each subplot was surveyed twice, while for the seed decay model we included seed species as the first nested random factor along with the others.

Data analysis: ecosystem services trade-offs and synergies

To evaluate trade-offs and synergies between ecosystem service indicators, we needed to have the same number of measurements for each indicator; we therefore calculated, for each plot, the mean values of the indicators that were measured multiple times per plot, so that they could be correlated with the indicators that were measured only once per plot. Additionally, some of our indicators (herbivore abundance, disease incidence, weed biomass, weed species richness) were actually indicators of ecosystem disservices, i.e. they were positively related to the success of noxious organisms. In order to calculate synergies and trade-offs, all indicators needed to be positively related with ecosystem services rather than with disservices. For disservices indicators, therefore, measures were transformed so that higher values corresponded to higher ecosystem services[34]. For instance, herbivore abundance measures were transformed into an indicator of herbivore control according to the formula $herbivore\ control = (Xmax - X)/Xmax$, where X is the value of each measure of herbivore abundance and $Xmax$ is the highest value of X in the dataset, resulting in an index ranging from 0 (minimum herbivore control in the studied context) to an ideal 1 (total herbivore control in the studied context). The same principle was applied to disease control, weed biomass control and weed diversity control. We calculated the index also for the latter, considering weed species richness as a measure of weed success against crops, for simplicity and coherence with the other indicators—although, as mentioned in the introduction, weed diversity can also have positive effects on agroecosystems[15,59].

Pairwise correlation coefficients are a simple and yet effective and widespread method to test for synergies and trade-offs between ecosystem services, including agricultural services[34,60]. We thus calculated Pearson correlations between the ecosystem service indicators for the conservation and conventional tillage datasets, and for the drought treatment and rainfed treatment datasets, separately. We did not consider the correlations between wheat yield and between organisms that were specifically sampled only on soybean (pests, predators, pathogens), nor the correlations of such organisms with weeds, as weeds were sampled after soybean harvest. We did consider the correlation between soybean yield and weed control (including seed decay) as crops can both influence soil microbial communities with long lasting consequences on crops that succeed them[61] and, by outcompeting weeds, they can limit weed contribution to seed bank and have legacy effects on the weed control in following seasons[62]. Analyses were performed using package *corrplot*[63] in R v3.6.2

Finally, to check the effect of tillage and drought stress on the overall provision of all the considered services, we used a Nonmetric MultiDimensional Scaling (NMDS) plot[64] and carried out an analysis of similarities (ANOSIM)[65], in both cases using Bray–Curtis distance[66] and using the *vegan*[67] package in R v3.6.2. All ecosystem service data were normalized into a 0 to 1 scale (were 1 represented the highest possible value of a given service in the dataset) for this analysis.

Results

Drought treatment, tillage regime and soil phosphorus had varying effects on the measured ecosystem service indicators – though for most indicators, interactions between explanatory variables were not significant and were thus removed from the models.

Crop yield

For soybean, crop yield was significantly lower in the drought treatment than in the rainfed control, with a 21% reduction (Table 1, Fig. 2a). Wheat yield, like soybean, was significantly lower in the drought treatment than in the rainfed control, with a 13% reduction (Table 1, Fig. 2b). Neither tillage regime nor soil phosphorus had significant effects on either crop yield.

Herbivores, predators and pathogens in soybean

Arthropod taxa surveyed in the study are reported in Supplementary Table S4. Tillage, drought treatment and phosphorous had no effect on herbivore or predator abundance (Table 1). Disease incidence, on the other hand, was higher in conventional than in conservation tillage, and this difference was more accentuated in the rainfed control (69%) than under drought conditions (53%) (Table 1, Fig. 3a). Disease incidence also steeply decreased with soil phosphorus content (Fig. 3b).

Seed decay

Seed decay slightly decreased with increasing soil phosphorus content (Table 1, Fig. 4a), while tillage regime and drought treatment had no effect.

Dependent variable	Random factors	Independent variables	Estimate	d.f	Chi-square	*P*
Model 1						
Soybean yield	Pair/field	Tillage	5.2	1	0.01	0.91
		Drought	− 53.07	1	10.00	< 0.01
		Phosphorus	− 1.94	1	0.50	0.48
Model 2						
Wheat yield	Pair/field	Tillage	41.72	1	0.34	0.56
		Drought	− 60.93	1	5.23	0.02
		Phosphorus	− 3.43	1	0.71	0.40
Model 3						
Herbivore abundance	Pair/field/plot	Tillage	− 0.41	1	2.39	0.12
		Drought	0.22	1	0.73	0.39
		Phosphorus	− 0.005	1	0.14	0.71
Model 4						
Predator abundance	Pair/field/plot	Tillage	− 0.15	1	0.29	0.59
		Drought	0.01	1	2.16	0.14
		Phosphorus	0.40	1	0.51	0.47
Model 5						
Disease incidence	Pair/field/plot	Tillage	3.16	1	9.51	< 0.01
		Drought	0.26	1	2.89	0.09
		Phosphorus	− 0.25	1	7.30	< 0.01
		Tillage*Drought	− 1.17	1	3.92	< 0.05
Model 6						
Weed seed decay	Pair/field/plot	Tillage	0.03	1	1.94	0.16
		Drought	− 0.01	1	0.62	0.43
		Phosphorus	− 0.002	1	4.91	0.03
Model 7						
Weed biomass	Pair/field/plot	Tillage	− 132.28	1	11.11	< 0.001
		Drought	122.49	1	9.97	< 0.01
		Phosphorus	7.56	1	8.56	< 0.01
Model 8						
Weed species richness	Pair/field/plot/subplot	Tillage	0.19	1	0.12	0.73
		Drought	0.79	1	6.72	< 0.01
		Phosphorous	− 0.04	1	2.55	0.11

Table 1. Results of the linear mixed effects models (Models 1–2, 6–8) and generalized linear mixed effects models (Model 3: Negative binomial, Model 4: Poisson, Model 5: Binomial) testing the effects of drought treatment, tillage regime and soil phosphorus content on the explanatory variables related to yield and weed, pest and pathogen control. Weed seed decay was square-root transformed to meet model assumptions. Estimates for "Tillage" and "Drought" were calculated using respectively conservation tillage and the rainfed control as the first level.

Weed biomass and diversity

The detailed list of weed species recorded in the study is reported in Supplementary Table S5. In the case of weed biomass, all three explanatory variables had significant effects with no interactions (Table 1). Conservation tillage, drought conditions and high phosphorous content all increased weed biomass separately (Fig. 4b–d), with increases caused by conventional tillage and drought being 26% and 27%, respectively. As for weed species richness, it increased (17%) with the drought treatment (Fig. 4e) with no significant effects of the other variables.

Ecosystem services trade-offs and synergies

The NMDS plot and the ANOSIM did not show any significant difference between tillage and drought treatments in terms of global ecosystem services provision, although tillage had a near-significant effect ($0.05 < P < 0.10$) (Supplementary Fig. S1). When considering pairwise correlations between services (Fig. 5), the drought scenario and conventional tillage presented a lower number of significant or near-significant trade-offs and synergies if compared to the alternative (normal rainfall and conservation tillage respectively).

The most frequent synergies were between soybean and wheat crop yield, and between the yield of these crops and weed control (either biomass or diversity), while the most frequent trade-offs were between soybean yield and indicators of pest control (either herbivore control or predator abundance).

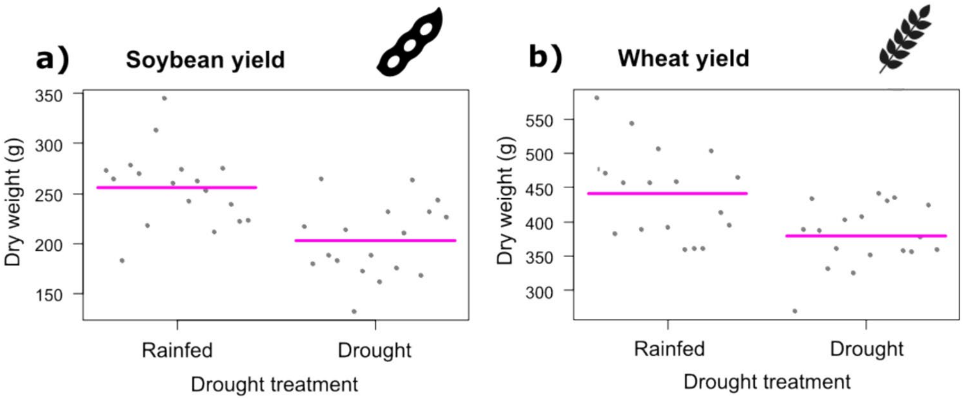

Fig. 2. Significant ($P < 0.05$) effects of drought treatment on soybean yield (**a**) and wheat yield (**b**) according to LMMs. Solid lines indicate model estimates, dots indicate partial residuals. Plots were generated using package visreg v2.7.0 in R. Explanatory variables and interactions that had non-significant effects are not shown.

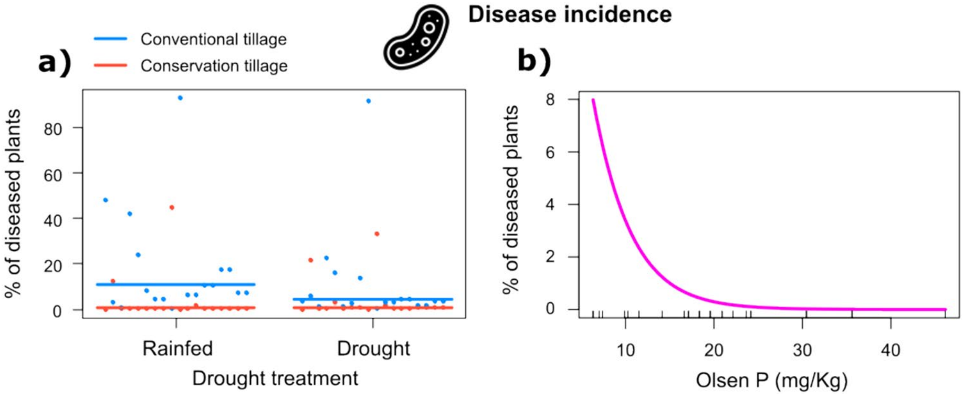

Fig. 3. Significant ($P < 0.05$) effects of the interaction of drought treatment and tillage regime (**a**), and of phosphorous content (**b**) on soybean disease incidence according to the binomial GLMM. Solid lines indicate model estimates, partial residuals are indicated by dots for (**a**) and a rug for (**b**). Plots were generated using package visreg v2.7.0 in R. Explanatory variables and interactions that had non-significant effects are not shown.

Discussion

Our study showed that drought, tillage regime and soil phosphorus content can influence crop yield as well as weed, pest and pathogen control. In particular, both conservation and conventional tillage presented strengths and weaknesses, while simulated climate change drought mostly had undesirable effects. As expected, drought treatment reduced the yields of both studied crops, which can at least partially be a direct effect of the increase drought stress on the plant[68]. Indirect effects mediated by the increase in harmful organism populations are likely to depend mostly on weeds. Weeds were indeed confirmed as one of the most critical factors to consider in modern day ecosystems as well as in future climate change scenarios[11,12]. Weed biomass production was especially boosted by drought, conservation tillage and soil phosphorous.

Before further discussing the results, it is worth mentioning a potential limitation of our study, which is the fact that we only measured each variable for a single year (either 2018 or 2019). One consequence of this fact is that our study is only fit to reveal relatively short-term effects of drought, while multiple-year studies may be needed to reveal long-term effects[69–71]. Additionally, crop yield, weed and insect populations, as well as ecosystem functions can fluctuate—sometimes dramatically—over time, in response to weather fluctuations, climate shifts and other environmental variables. Studies aiming at fully capturing this variability are usually repeated for 5 or more years[72–74], a time frame which was outside the scope or the budget of our project. The space-for-time approach, replacing temporal replication with spatial replication, is popular for studies focusing on long-time trends such as the effects of climate change[75]; similarly, the relatively high number of sampled sites spread across different areas of the study region ensures that we captured some degree of environmental variability in spite of the single-year samplings, improving the generalizability of our results. Nonetheless, our conclusions remain valid for the climate and environmental conditions found in the study areas in the sampling years, and further generalizability would require additional, longer-term experiments.

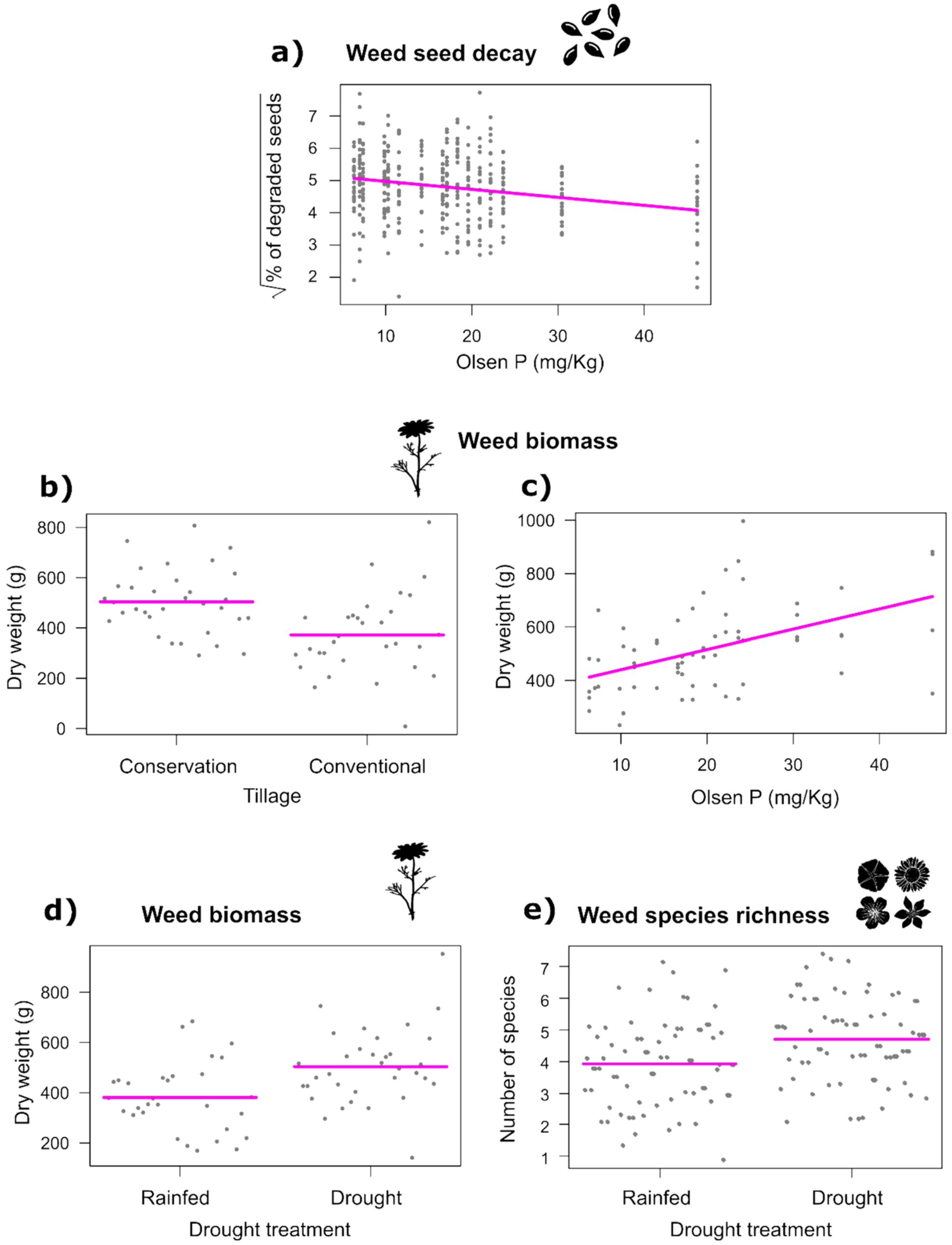

Fig. 4. Significant ($P < 0.05$) effects of explanatory variables on weed control parameters, including interred weed seed decay (**a**), weed biomass (**b**–**d**) and weed biodiversity (**e**) according to LMMs. Seed decay incidence was square-root transformed to meet model assumptions. Solid lines indicate model estimates, dots indicate partial residuals. Plots were generated using package visreg v2.7.0 in R. Explanatory variables and interactions that had non-significant effects are not shown.

Drought treatment did not affect herbivore abundance, in contrast with studies showing a positive effect[25,76]. Effects on herbivores may require a longer period of drought to become apparent[69,70]. While some studies had reported negative effects on natural enemies[77], others showed that climate change conditions, including drought, can occasionally increase natural enemy populations or biological control[78]. In our case, however, while predatory arthropods were more abundant in drought conditions, the difference was not significant, making it unlikely that they played a role in the lack of increase in pest arthropod numbers. Additionally, neither pests nor predators were influenced by tillage regime or soil phosphorus.

Disease incidence was influenced by tillage regime, with conventional tillage fields being more affected by crop pathogens than conservation tillage. This stands in contrast with a sizeable portion of the available literature, according to which conservation tillage practices makes crops more susceptible to disease[79,80], although some sources also report lower disease incidence in conservation tillage[81], which could be linked with a higher abundance and richness of non-pathogenic microorganisms competing with pathogens[82,83]. These discrepancies might be caused by differences in the physiological state of the crops, which may alter their susceptibility to

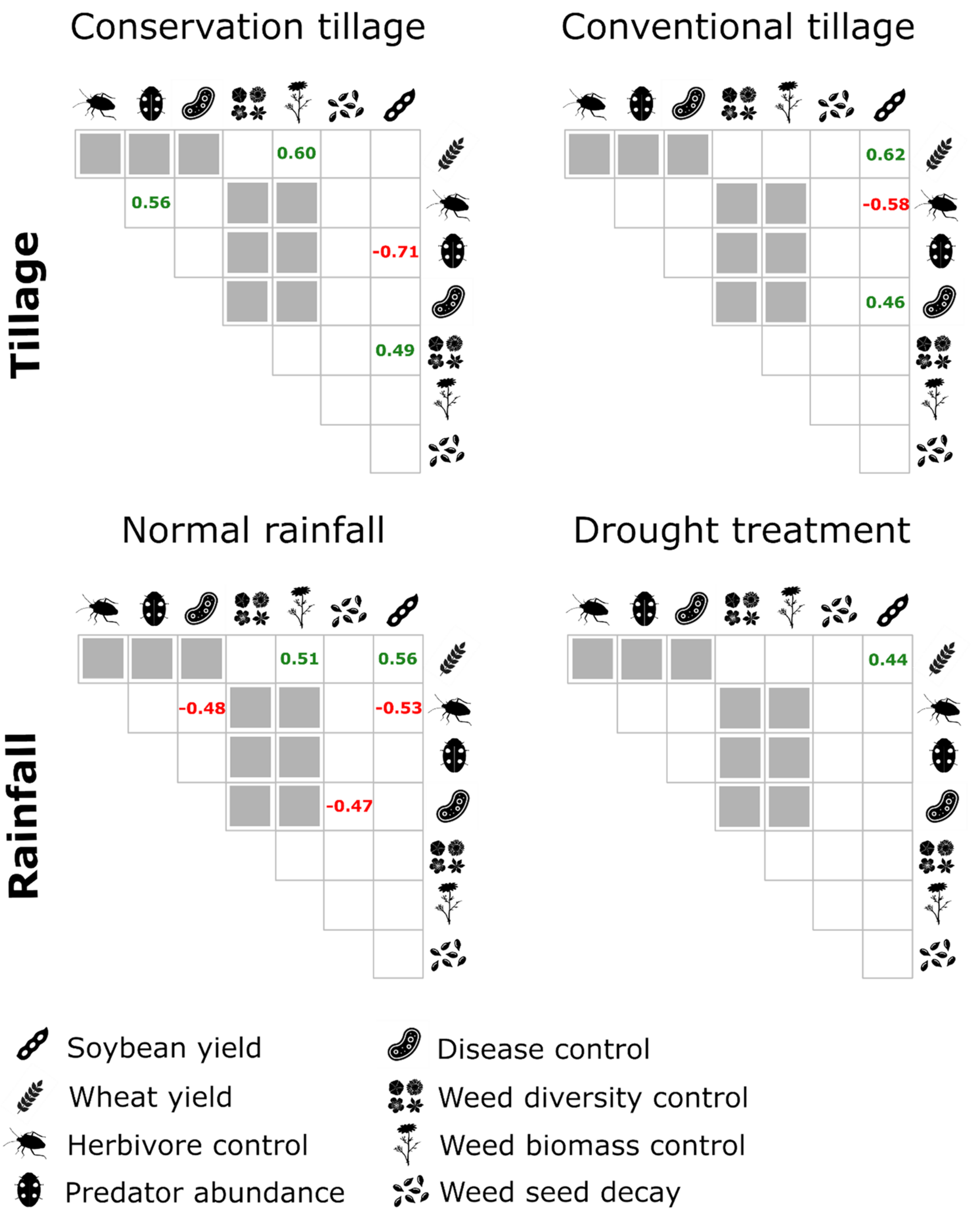

Fig. 5. Significant ($P < 0.05$) and near-significant ($0.05 < P < 0.10$) trade-offs (in red) and synergies (in green) between ecosystem service indicators in the two tillage regimes (upper row) and in the two rainfall scenarios (lower row). We report the value of the Pearson correlation coefficients between services. Grey squares represent relationships that were not tested due to variables being measured in different seasons.

infection[31]. For instance, conservation tillage is known to improve soil water conservation and reduce drought stress[84], which is particularly important in arid conditions. This might mean that, in a future climate change scenario with increasing droughts, the recorded higher susceptibility of conventional tillage crops to disease might be furtherly exacerbated. It should however be noted that the drought treatment reduced disease incidence in conventional tillage (although it remained higher than in conservation tillage). This might be explained by a lower residual humidity on leaves in drought conditions, as leaf humidity favors leaf pathogens[31]. Considering also our results on drought, this factor might be more important than a possible increased susceptibility caused by drought, even potentially reducing the pathogen problems of conventional tillage agriculture. The clear trend of disease incidence steeply decreasing with soil phosphorus content is in line with most of the literature on the subject, which reports that phosphorus often improves plant health either through direct effects on pathogen multiplication or effects on plant metabolism and defenses[85].

Weed biomass and richness were influenced by multiple factors. As expected, weed biomass was in general higher in conservation than in conventional tillage[12,42] and, alongside weed species richness to a lesser degree, was positively influenced by drought conditions favouring hardy, drought-resistant weed species over the crops. While there was no significant interaction between these two explanatory variables, it is likely that, in future climate change scenarios, conservation tillage fields will be at a higher risk of suffering from problems related to weed biomass increases if compared with conventional fields, requiring efficient weed control strategies, such as thick mulching and robotic weeding, to remain viable without herbicide overuse. It is however important to note that usually cover crops are included in the conservation tillage regime also as a weed control strategy[86], and this element was not incorporated in our manipulative experiments.

Soils with high phosphorus content generally increased weed biomass production. Phosphorous is indeed a nutrient that is more efficiently exploited by weed species rather than crops[87]. However, another factor may be at play, as phosphorus was also linked with lower buried seed decay. While the design of our study is not fit to provide a definite mechanistic explanation of this phenomenon, it is known that phosphorous can influence soil microbial communities, and while this influence is generally regarded as beneficial, in some conditions it might shift community composition in a way that alters certain ecosystem functions[88]. This might mean that weed control through seed decay would be increasingly inefficient in soils with high phosphorous content. Overall, conventionally tilled fields in low-phosphorus soils might be at a lower risk of weed-related problems in increasingly dry conditions.

Altogether, drought at the levels tested in our experiment did not significantly alter the overall provision of the suite of ecosystem services that we studied, while tillage only had a near-significant effect. When considering specific pairwise correlations between services, however, it appears that stressful environmental factors—both drought conditions and conventional tillage—reduce the number of significant or near-significant ecosystem service indicator trade-offs and synergies, similarly to what was reported by Tamburini et al. (2016)[34] for conventional tillage and artificial fertilization. In climate change drought conditions, due to the observed loss of positive associations between ecosystem services, it could thus become more difficult to improve multiple services with a single management action, and each service might require a specifically tailored action. In that scenario, such management actions would nonetheless have a lower chance of negatively impacting non-target services, due to reduced negative associations among them.

Synergies between soybean yield and wheat yield indicate that these different crop types tend to be positively influenced by a similar set of variables. Alongside that, synergies between crop yield and weed biomass/diversity control were relatively common. This is in line with our initial expectations and, when considering the interaction between weeds and wheat, it further confirms the role of weeds as the main biotic limiting factor for crops. When considering the interaction between soybean and weeds, the relatively common yield/weed control synergies also confirm the importance of successful crop competition against weeds in limiting weed incidence in the following seasons. On the other hand, the most common trade-offs were between soybean yield and pest control, in the form of either herbivore suppression or predator abundance, which seems to indicate that increasing crop success might result in more severe pest infestations. Additionally, soybean success in conventional tillage was linked simultaneously with an increase in the control of weed diversity and a decrease in the number of arthropod predators; as we hypothesized, since weed diversity can support biological control agents by offering favorable microhabitats and alternative prey[14], success in weed control might result in negative consequences for pest control in some instances.

Conclusions

Our results highlight some important consequences of drought on crop yield and multiple parameters related to weed, pest and pathogen control, as well as the potential effects of soil management regime through tillage and soil phosphorus content, paving the way for future research lines. Experiments focused on the potentially interactive effects of multiple environmental factors on yield are pivotal, given the importance of the topic for agricultural productivity in a rapidly transforming world, and our still limited knowledge of the topic[89]. Contrary to expectations, the effects of conservation tillage on ecosystem services and drought mitigation were mixed, suggesting a challenging path ahead for climate change adaptation. Weeds were confirmed to be the most likely biotic limiting factors for crops in climate change scenarios. Sustainable weed management strategies will become increasingly important, especially for conservation tillage fields, which are more susceptible to weeds. The use of fast-growing cover crops able to outcompete weeds[90], the protection of seed predator communities[36] and the correct management of soil for enhancing seed-degrading microorganisms[18] might all represent promising ways of mitigating the problem without an increase in herbicide use, all while continuing to reap some of the benefits associated with conservation tillage (including improved disease control). Soil phosphorous seems to be an important variable which might require a fine tuning to balance between its desirable (disease control) and undesirable effects (weed increase, possibly also through seed decay reduction). There is indication, however, that this type of trade-offs (and synergies) between ecosystem services will be less frequent under climate change conditions, especially in conventionally tilled fields, implying that we will require complex combinations of interventions to reduce the negative effects of drought, weeds and pests.

Data availability

The datasets generated and analyzed during the described study are available from the corresponding author on reasonable request.

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Author contributions

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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