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Larger yields of mixtures than monocultures of cultivated grassland species match with asynchrony in shoot growth among species but not with increased light interception

Sébastien Husse[a,b], Olivier Huguenin-Elie[a,*], Nina Buchmann[b], Andreas Lüscher[a]

[a] Agroscope, Institute for Sustainability Sciences, Reckenholzstrasse 191, 8046 Zürich, Switzerland
[b] ETH Zürich, Institute of Agricultural Sciences, Universitätstrasse 2, 8092 Zürich, Switzerland

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ABSTRACT

Optimizing agricultural benefits of mixtures as compared to monocultures requires identification of effective combinations of plant species characteristics. To understand processes of yield formation in cultivated grasslands we assessed the effect of mixing four forage species with contrasting foliar architecture and seasonal shoot growth. The yield of each species and its seasonality, instantaneous and cumulative light interception, as well as the stratified leaf area index were measured in monocultures and 11 types of mixtures of four key species of productive temperate grasslands worldwide: *Lolium perenne*, *Cichorium intybus*, *Trifolium repens* and *Trifolium pratense*. The mixture with equal sown proportions of each species achieved 23–31% higher total yield than expected from the monocultures (mixture effect). Over the three experimental years, mixture yield was positively correlated to the seasonal asynchrony in shoot growth between component species ($r = 0.76$, $P < 0.001$). In contrast, there was no mixture effect on instantaneous light interception at the end of regrowth periods: light interception was almost complete ($\geq 90\%$) for all sward types at the end of six of the eight regrowth periods examined, also for monocultures (except for *L. perenne*). This leaves no potential for further improvement of light interception in mixtures. In the middle of the regrowth periods, when light interception was not yet complete, a mixture effect on instantaneous light interception was detected. However it was too small and too short-term to translate into mixture effects on light interception cumulated over the whole regrowth period. These results indicate that to achieve positive mixture effects on yield in productive cultivated grasslands, mixing species asynchronous in seasonal shoot growth is more important than mixing species with contrasting foliar architecture.

1. Introduction

Various experiments with cultivated grasslands have shown that mixtures of plant species with contrasting characteristics produce larger yields compared to the weighted average of the monocultures of their component species (mixture effects; Sanderson et al., 2004; Finn et al., 2013). Such increased yields at the same level of resource inputs are an important contribution to sustainable intensification, a major challenge of nowadays agriculture (Foley et al., 2011) and may be explained by the processes of niche differentiation and facilitation in the use of resources (e.g. Hooper et al., 2005; Roscher et al., 2011). These processes depend on below- and aboveground characteristics of the plant species occurring in the sward (Hooper et al., 2005; Anten and Hirose, 1999). However, studies on mixture effects in cultivated grassland swards mainly focussed on symbiotic nitrogen fixation (Nyfeler et al., 2011; Suter et al., 2015). It thus remains unclear if cultivated mixed swards benefit from the association of species with different aboveground characteristics.

In low productivity swards combining species from semi-natural permanent grasslands, greater species richness resulted in higher light interception (Spehn et al., 2000). This larger light interception in mixed swards compared to monocultures may be due to greater Leaf Area Index (LAI). Indeed, Roscher et al. (2011) showed higher LAI at the community level with greater species richness. Light interception through a canopy follows a function of the shape $(1 - e^{-k \cdot \mathrm{LAI}})$ and thus, the increase in light interception with increasing LAI is much larger at small LAI than at LAI above 3 (Monsi and Saeki, 1953). Consequently, because large differences in LAI have been observed between low productivity swards

* Corresponding author.
E-mail address: olivier.huguenin@agroscope.admin.ch (A. Lüscher).

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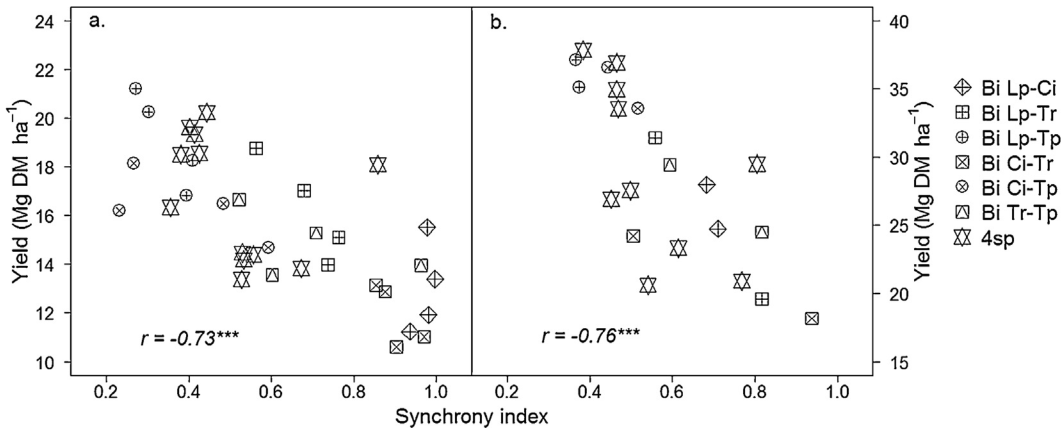

Fig. 1. Total yield as a function of the synchrony index for the 2-species and the 4-species mixtures (a) over the first 13-months period and (b) over the three experimental years. Each point corresponds to a plot. For the abbreviation of sward types, refer to Table 1. *r*: Pearson correlation coefficient. *** $P < 0.001$.

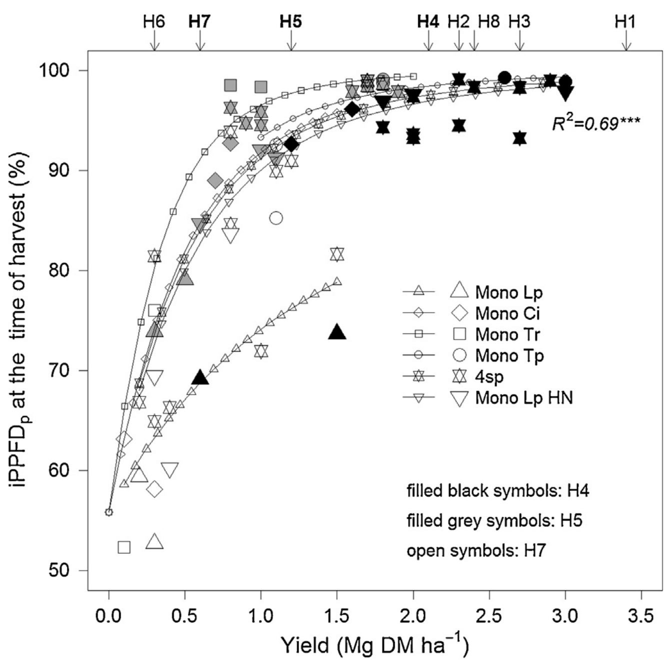

Fig. 2. Percentage of incident PPFD intercepted at the time of harvest (iPPFD$_p$) as a function of yield. The lines correspond to the back-transformed linear regressions performed on the transformed data (logit(iPPFD$_p$), log(Yield)) for each sward type over the three studied harvests. The average yield over all sward types is indicated at the top of the figure for each of the eight harvests (arrows). H#: #th harvest. For the abbreviation of the sward types, refer to Table 1. *** $P < 0.001$.

(LAI < 2.8; Spehn et al., 2000) and productive swards (LAI up to 8; Suter et al., 2001), results about effects of species richness on light interception cannot be extrapolated from the former to the latter. We thereafter refer to fertilized grasslands with high yielding species as productive cultivated grasslands in opposition to low productivity semi-natural grasslands.

In the event of nearly complete light interception by the canopy, light can be considered as unidirectional, competition for light is size-asymmetric (Schwinning and Weiner, 1998), and the leaves at the top of the canopy intercept a high proportion of the incident light (Hautier et al., 2009). However, mechanisms of light competition in such crowded plant populations remain unclear (Berntson and Wayne, 2000; Weiner and Damgaard, 2006). For instance, Yachi and Loreau (2007) showed that mixing species with different foliar architecture contributed to less light competition and higher biomass production compared to monocultures, and yet the shifts in botanical composition resulting from plant competition either reinforced or counteracted the benefit on biomass. Certain studies have analyzed the effects of combining species with different aboveground characteristics on light interception and biomass production in cultivated swards (Vojtech et al., 2008; Frankow-Lindberg and Wrage-Mönnig, 2015). Vojtech et al. (2008) showed that mixtures that combine grass species with contrasting foliar architecture slightly improved light interception and biomass production compared to monocultures. Mixture effects on light interception might nevertheless be larger when mixing species with wider differences in their foliar architecture than *Poaceae* among themselves. Indeed, Frankow-Lindberg and Wrage-Mönnig (2015) showed a clear benefit of mixing grasses and *Cichorium intybus* L. with legume species on light interception compared to grass monocultures. However, their study focused on the differences between legumes and non-legume species and did not analyze the potential mixture effects between species. The effects of adding non-legume broad-leaved forbs to cultivated intensive grasslands thus remain unknown.

Differences in seasonal productivity of the species of the community may lead to temporal complementarity in light interception (or any other resource) at the scale of multiple regrowth periods during the whole growing season (Anten and Hirose, 1999). If the peaks of productivity of each species of the community are asynchronous, this may maintain a stable level of productivity throughout the year (Isbell et al., 2009), which in the case of competition for light, could promote a high annual biomass yield (Loreau and Hector, 2001). Moreover, experiments in low productivity swards showed that within the canopy, differences in leaf distribution between species also allow better light interception along the canopy (spatial complementarity; Lorentzen et al., 2008; Wacker et al., 2009) and that the differences in leaf characteristics among species at the beginning of a regrowth lead to less competition for light (Anten and Hirose, 1999; Werger et al., 2002). However, it remains unknown whether such processes of temporal and/or spatial complementarity are important in productive cultivated swards that exhibit nearly complete light interception.

The aims of our experimental field study in model swards of cultivated grasslands were to assess the effects of mixing forage species with contrasting foliar architecture and seasonal shoot growth on light interception and yield during individual regrowth periods as well as over the three years duration of the experiment, to understand processes of yield formation, specifically to evaluate whether mixture effects on yield are associated with light interception and/or asynchronous seasonality of growth.