The revision for ***EEB-D-16-00822***

Influence of soil qualities on intra- and interspecific competition dynamics of *Larix kaempferi* and *L. olgensis*

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Running head: Effect of soil qualities on competition in *Larix*

Abstract Forest management has potential to detrimentally impact long-term plantation productivity. Establishment of mixed plantations and fertilization are two important management approaches when trying to maintain soil qualities and productivity. In this study, two types of experiments were conducted to investigate the influence of soil qualities on intra- and interspecific competition dynamics in two larch species. Experiment 1: We transplanted two deciduous larch species, *Larix kaempferi* and *L. olgensis*, to study intra- and interspecific competition dynamics in two different types of soil: one from a *c.* twenty years old *L. kaempferi* plantation (named larch soil) and another from a secondary natural forest (named mixed-forest soil). Experiment 2: Effects of N fertilization on the competition dynamics of the two larch species were tested in the larch soil. In the experiment 1, we hypothesized that the growth of *L. kaempferi* in the larch soil under no fertilization is inhibited when competing with *L. olgensis*, and their competition relationships may be different in the mixed-forest soil. In both species, the starch and TNC (total non-structural carbohydrate) concentrations of roots and shoots were significantly higher in the mixed-forest soil when compared to the concentrations in the larch soil without N fertilization (N-). The relative competition intensity (RCI) was affected by the soil type. RCI of *L. olgensis* was higher than that of *L. kaempferi* in the larch soil N- condition, and RCI of *L. kaempferi* was higher than that of *L. olgensis* in the mixed-forest soil in 2015. However, the RCI values did not show significant differences in 2014. In the experiment 2, *L. kaempferi* showed superior competitiveness in the larch soil N+ condition, with the highest RCI value in 2014,

but the RCI value of *L. kaempferi* declined while the RCI value of *L. olgensis* increased from 2014 to 2015. Both experiments indicated that the benefiting species had higher element (C, N and P) and non-structural carbohydrate (starch and soluble sugar) content accumulation ratios from 2014 to 2015. We found that competition relationships changed between years and depending on conditions. We suggest that mixed plantations and N fertilization together could effectively promote the productivity of *Larix*.

Key-words: non-structural carbohydrate storage · environmental heterogeneity · temporal niche differentiation · forest management · forest plantation

1. Introduction

Although the total area of forests is declining globally, different types of forest plantations are increasing. Forest plantations provide wood products to meet the social and economic demands and help to restore degraded land (Paul et al., 2010; Gong et al., 2013). Yet, forest management has the potential to detrimentally impact long-term plantation productivity. The paper by Keeves (1966) drawed attention to potential productivity declines in successive rotations of *Pinus radiata* and, thereafter, many other studies have revealed similar results in different types of plantations around the world (reviewed by, e.g., Fox, 2000; O'Hehir and Nambiar, 2010). Several methods are available to solve such forest management problems. The establishment of mixed plantations and the use of fertilization are two important management approaches to maintain soil qualities and plantation productivity (Fox, 2000; O'Hehir and Nambiar, 2010; Richards et al., 2010).

The benefits of mixed-forest plantations are probably due to interactions between species or interactions with soils that are not present in monoculture plantations (Richards et al., 2010; Guo et al., 2016). Types of plant-plant competition (positive, negative or neutral) frequently shift or change in response to different environmental factors. As previously shown, spatial and temporal environmental heterogeneity can alter competitive relationships (Sthultz et al., 2007; Maestre et al., 2009; Soliveres et al., 2010; Liu et al., 2013; Biswas and Wagner, 2014). Species can distinguish

conspecific and heterospecific individuals, and this may lead to substantial changes in interactions (Schmid and Kazda, 2002; Miller et al., 2007; Duan et al., 2014). Competitive responses are dynamic processes and they have been examined by many modelers (e.g., Damgaard et al., 2002; Crone, 2016). Several experiments have confirmed temporal changes in competition by measuring simultaneous changes in resource capture and biomass production (e.g. Trinder et al., 2012a, b). Typical one-time biomass measurements cannot provide unambiguous insights into the competition dynamics of plants.

After several successive rotations, forest plantations typically show declined soil qualities, for example, lowered N availability to plants (Fox, 2000; O'Hehir and Nambiar, 2010). Thus, fertilization is an important way to ameliorate plantation soil qualities and promote productivity. Soil nutrient availability limits ecosystem productivity, either on their own or in combination with other mineral nutrients (Wassen et al., 2005). Plants have been shown to display different root distributions between conspecific and heterospecific species for resource capture (Schmid and Kazda, 2002). Many experiments have confirmed that plants' competitive interactions vary along with the availability and form of N or P (Maestre et al., 2005; Trinder et al., 2012b; Ahmad-Ramli et al., 2013; Wilberts et al., 2014), and negative competition reduces species richness (Hautier et al., 2009). Also, effects of forest plantations on soil microbial community structures could be an important reason that affects soil qualities and productivity. He et al. (2014) have shown that after the replacement of a

natural broadleaf forest, bacteria with a close phylogenetic relationship to *Pedobacter cryoconitis* disappear, but those with a close phylogenetic relationship to *Xanthomonas spp.* and *Rhodanobacter spp.* begin to appear in the soil of a *Cunninghamia lanceolata* plantation.

The accumulation of N pools affects the performance and growth of plants (Jordan et al., 2012, 2014). Non-structural carbohydrates, the sum of soluble sugars and starch, play a key role in physiological processes, such as serving as signaling molecules, providing basic C energy to growth and respiration (Koch, 2004; Secchi and Zwieniecki, 2011) and maintaining cell turgor and osmoregulation (Muller et al., 2011). It has been shown that non-structural carbohydrate storage can enhance plants' ability to resist stress conditions (Myers and Kitajima, 2007; Wiley et al., 2013; O'Brien et al., 2014). Non-structural carbon pools positively correlate with survival, especially when seedlings experience shade and defoliation (Myers and Kitajima, 2007). Species differ in the ways they produce, use, store and allocate non-structural carbohydrates, and this may determine their competitive ability. A few studies have found that intra- and interspecific competition modulates the concentration or accumulation of starch or soluble sugars (Liu et al., 2004; Duan et al., 2014; Guo et al., 2016). Differences in sizes of carbon pools are important functional traits that may reflect plants' competitive ability.

In this study, we conducted experiments to investigate intra- and interspecific

competition dynamics in two deciduous tree species *Larix kaempferi* (Lamb.) Carr and *L. olgensis* A. Henry under two different soil types and under N fertilization. These two species are closely similar in life history traits and morphological traits, which make them difficult to be distinguished from each other, especially at the juvenile stage. However, they show differences in the growth rate, photosynthetic rate and N-use efficiency (Li et al., 2016). In the Experiment 1, we used one kind of soil from the *L. kaempferi* plantation and another type of soil from a natural secondary forest. We aimed to reveal the effects of the two soil types on competition dynamics. We hypothesized that the growth of *L. kaempferi* in the *L. kaempferi* soil under no fertilization is inhibited when competing with *L. olgensis*, and their competition relationships may be different in the soil sampled from the natural secondary forest. There is previous knowledge that a particular species may decline its growth in its own soil, while the growth of another species may not be negatively affected (Bever et al., 2012; Hendriks et al., 2015). In the Experiment 2, we studied the effects of N fertilization on the competition dynamics of the two larch species in the larch soil. Previously, Li et al. (2016) have shown that N fertilization promotes the growth of *L. kaempferi* in the *L. kaempferi* soil. We wanted to know, whether N fertilization would affect the competitive performance of the two larch species grown in the *L. kaempferi* soil. Finally, we wanted to know how the plants' nutrition and non-structural carbohydrate accumulation are affected by competition.

2. Methods and materials

2.1. Study site and experimental design

Our study was conducted at the Qingyuan Experimental Station of the Forest Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, located in a mountainous region in the eastern Liaoning Province, Northeast China (41º51'N, 124º54'E). Larch forests are the dominant forest plantation type through northeastern Asia to central Siberia (Liang et al., 2004). The studied species, *L. kaempferi* and *L. olgensis*, are the major plantation tree species in cold and medium temperate zones of China. Two different soil types were used and they originated from a *c.* twenty years old planted forest community of *L. kaempferi* and from a natural secondary forest community. *Quercus mongolica* and *Juglans mandshurica* are the dominant tree species in the natural secondary forest. Hereafter, we call the two types of soil larch soil and mixed-forest soil, respectively. The sampled soil was homogenized before planting. The two types of soil were different in their physical and chemical properties. The former type of soil (pH 5.65, C 18.61 g kg^{-1}, N 1.82 g kg^{-1}, P 4.38 g kg^{-1}) is light brown and the percentage of gravel (> 2 mm) averages 7.28%, while the latter type of soil (pH 6.24, C 42.78 g kg^{-1}, N 3.89 g kg^{-1}, P 6.01 g kg^{-1}) is dark and the percentage

of gravel averages 21.37%.

2.2. Experiment 1: two soil types

The intra- and interspecific competition treatments were designed as follows: monoculture plantations reflecting intraspecific, competition *L. kaempferi* + *L. kaempferi* and *L. olgensis* + *L. olgensis*; mixed cultures representing interspecific competition, *L. kaempferi* + *L. olgensis*. This experiment aimed to reveal the soil effect on the competition dynamics of the two species. Three competition treatments and two soil types (larch and mixed-forest soil) were set up.

2.3. Experiment 2: N supplied to the larch soil

Effects of N fertilization were tested only in the larch soil. Urea (46.3% N) was used for N fertilization (as in Zhu et al. 2011) in the monocultures and mixed plantations of both species using larch soil. We added urea twice a year, in May and June (5.1 g each time) during years 2014 and 2015. The urea was homogeneously applied to each pot, which were immediately watered. Three competition treatments and two N conditions (with and without N fertilization) were set up. Thus, in the larch soil, there were three treatments without N fertilization: two monoculture plantations (Mo), one for each species, and one mixed culture (M), and three additional treatments with N fertilization: two monoculture plantations, one for each species (PN) and one mixed

plantation (MN). Competition treatments were the same as in experiment 1. The three treatments without N fertilization in experiment 2 were the same as the three treatments in the larch soil in experiment 1.

One-year old seedlings with approximately the same crown size and height (no significant statistical differences) were selected from a local nursery garden. In late October, 2013, two seedlings were planted in each plastic pot (external diameter and height 56 cm and 33 cm, respectively) to set up intra- and interspecific competition treatments for both species using two different types of soil (*c.* 70 kg soil per pot). Sixteen replicates per treatment were included in the study. Additionally, three individuals of each species were grown singly (S) in each type of soils and in the N fertilized larch soil (SN).

2.4. Harvesting and measurements

We harvested plants twice, on the 29th of August, 2014 and 4th of September, 2015. In 2014, four pots from each treatment were randomly harvested and all individuals were divided into leaves, shoots and roots. In 2015, four or five pots from each treatment were selected and the harvested individuals were divided into leaves, branches, stems, coarse roots (diameter > 2 mm) and fine roots (diameter < 2 mm). All harvested plants were dried at 70 °C for 72 h. Three replicates from single plantation patterns (S and SN) were harvested only in 2015. All dried materials were ground into a power for

1 further measurements.

2

3 We measured the concentrations of C, N, P, starch and soluble sugars in each part of
4 the harvested materials. The C, N and P concentrations were determined by the rapid
5 dichromate oxidation technique (Nelson and Sommers, 1982), the semi-micro
6 Kjeldahl method (Mitchell, 1998) and the vanadate-molybdate yellow colorimetric
7 method (Yang et al., 2011) after minor modifications. Methodological details of the
8 measurements of starch and soluble sugars were described by Guo et al. (2016).

9

10 *2.5. Data analysis*

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12 Firstly, we calculated the relative competitive intensity (RCI) of both species when
13 exposed to different competition treatments, N fertilization or soil types in 2014 and
14 2015, according to the formula described by Grace (1995) as follows:
15 RCI = Bc – Bs / Bs
16 Where Bc represents the total biomass of an individual from interspecific competition
17 and Bs represents the average total biomass of corresponding plants from intraspecific
18 competition. Positive RCI value stands for a better growth with a heterospecific
19 species than with a conspecific one.

20

21 Secondly, we calculated the concentration dynamics of C, N, P and non-structural
22 carbohydrates (starch, soluble sugars and total non-structural carbohydrates TNC) of

each plant organ during both years. TNC of each organ was the sum of its starch and soluble sugars. The formula was as follows:

Concentration variation = [$Concentration_{2015}$ – $Concentration_{2014}$] / $Concentration_{2014}$, where $Concentration_{2015}$ and $Concentration_{2014}$ represented the concentrations of C, N, P and non-structural carbohydrates in 2015 and 2014, respectively. In 2015, we defined the shoot as the sum of branches and stems. Concentrations of shoots were calculated as follows:

Concentration = [Bio_{Branch} × $Concentration_{Branch}$ + Bio_{Stem} × $Concentration_{Stem}$] / [Bio_{Branch} + Bio_{Stem}], where Bio_{Branch} and Bio_{Stem} represent branch and stem biomasses, respectively.

Similarly, concentrations of roots were computed as follows:

Concentration = [Bio_{Coarse} × $Concentration_{Coarse}$ + Bio_{Fine} × $Concentration_{Fine}$] / [Bio_{Coarse}+ Bio_{Fine}], where Bio_{Coarse} and Bio_{Fine} represent biomasses of coarse and fine roots, respectively.

Changes in the contents of C, N, P and non-structural carbohydrates (starch, soluble sugars and TNC) were calculated as follows: Content accumulation = [$Content_{2015}$ – $Content_{2014}$] / $Content_{2014}$, where $Content_{2015}$ and $Content_{2014}$ represent the contents of C, N, P and non-structural carbohydrates in 2015 and 2014, respectively. The content of each plant part, for instance, the leaf N content of an individual was obtained by multiplying the leaf N concentration by leaf biomass. In 2015, the contents of shoots were the sum of branch and stem contents.

Data were checked for normality and the homogeneity of variances. Parameters were log-transformed when needed. Tukey's *b* tests were carried out for each species to detect their RCI differences among treatments. Three-way analyses of variance (ANOVA) were performed for individuals grown in the larch soil to detect the effects of species, competition treatment and N fertilization. When significant interactions were observed, Tukey's *b* tests were conducted as post hoc tests to discover significant differences among treatments. Similarly, two-way analyses of variance were performed for individuals grown in the mixed-forest soil to discover the effects of species and competition patterns. If a significant factor interaction between species and competition was found, Tukey's *b* tests were conducted as well. In order to discover the effects of soil type, an Independent-Samples T test was conducted for the same species in the same competition treatment but grown in two types of soil. All data were analyzed with the software Statistical Package for the Social Science (SPSS) version 20.0.

3. Results

3.1. Relative competitive intensity

The results showed that the relative competitive intensity (RCI) of the two species was influenced by the competition treatment, N fertilization or soil type. More importantly, RCI showed considerable temporal changes from 2014 to 2015 (Fig. 1). In 2014, the RCI value of *L. kaempferi* was significantly higher when grown with *L. olgensis* in the N-fertilized larch soil than in other treatments, while no other treatment differences were detected. Thus, the growth of *L. kaempferi* was facilitated by *L. olgensis* under N fertilization (Fig. 1a). In 2015, the RCI value of *L. olgensis* was higher than that of *L. kaempferi* in the larch soil N-, whereas the RCI of *L. kaempferi* was higher than that of *L. olgensis* in the mixed-forest soil (Fig. 1b). During the second year, after N fertilization in the larch soil, the RCI of *L. kaempferi* was still higher compared to that of *L. kaempferi* in the larch soil N-. However, the RCI of *L. olgensis* was higher compared to that of *L. olgensis* in the mixed-forest soil (Fig. 1b).

When compared with individuals grown alone without any competition, intra- and

interspecific competition declined the biomass of both studied species (Table 1). In the larch soil N+ condition, the growth of *L. kaempferi* was much greater under MN (mixed culture with N fertilization) and it exhibited significantly higher biomasses of coarse roots, fine roots, total roots and whole individuals when compared with PN (monoculture with N fertilization). A positive growth response was found also in the mixed culture (M) in *L. olgensis*, whose biomasses (e.g. branches and leaves) were significantly higher than those of plants grown in the monoculture (Mo) in the larch soil N- condition. However, the relationship shifted between the two species in the mixed-forest soil. Specifically, the growth of *L. kaempferi* greatly benefited from the presence of *L. olgensis*, as a greater total biomass difference between M and Mo was detected (Table 1).

3.2. Concentration variation

Single factors (competition, species or N fertilization) or their interactions caused temporal variation in C, N and P concentrations, except for the concentration of leaf C and shoot C in different soil types (see Table S1 in Supplementary materials). In the larch soil N- condition, the root C concentration of both species was significantly greater in mixed cultures (M) compared to monocultures (Mo), and this difference disappeared in the larch soil N+ condition (Fig. 2a). The leaf N concentration of *L. kaempferi* from the monoculture (Mo) was significantly higher than that of individuals grown under interspecific competition (M) in the larch N- soil (Fig. 2b).

In the mixed-forest soil, both leaf and shoot N concentrations of *L. olgensis* from mixed culture (M) were significantly lower compared with *L. olgensis* grown in monocultures (Mo) (Fig. 2b). The shoot P concentration of *L. kaempferi* from MN was significantly lower compared with the same species from PN in the larch soil N+ condition (Fig. 2c). N and P concentration variation between the two soil types were also observed, for example, leaf N and leaf P concentrations of *L. kaempferi* from the mixed culture (M) in the mixed-forest soil were significantly higher than those of *L. kaempferi* from the mixed culture (M) in the larch soil N- condition (Fig. 2b, c).

In larch soil N- condition, concentrations of shoot starch, soluble sugars and TNC as well as of leaf starch and TNC of *L. kaempferi* from mixed culture (M) increased more than those of individuals from *L. kaempferi* monoculture (Mo); by contrast, concentrations of root soluble sugars and root TNC of *L. kaempferi* were significantly higher in Mo (Fig. 2d, e, f). In *L. olgensis*, a significant concentration change was found only in root starch, which was higher in M than in Mo in the larch soil N- condition (Fig. 2d). In the mixed-forest soil, significant interactions of competition and species concerning the starch concentration of shoots and roots were observed (Table S1). Concentrations of root starch, root soluble sugar and root TNC of *L. kaempfer* from the mixed culture were significantly higher in the mixed-forest soil compared with those of *L. kaempfer* in the larch soil N- condition (Fig. 2d, e, f).

3.3. N and P pool sizes and accumulation dynamics

Different factors (competition, N fertilization and species) alone or their interactive effects influenced C, N and P contents of plant organs, as well as those of whole plants in different soils (Tables S2, S3 and S4 in Supplementary materials). We discovered that the growth of *L. kaempferi* greatly benefited from the presence of *L. olgensis* in the mixed-forest soil and it tended to have a significantly higher C accumulation or N pool size in leaves and shoots and in the whole individual (Tables S2 and S3).

In the larch soil N- condition, C, N and P content accumulation ratios of roots and shoots of *L. olgensis* were significantly higher in the mixed culture (M) when compared with monoculture (Mo), while *L. kaempferi* in the mixed-forest soil exhibited similar values in the mixed culture and monoculture (Fig. 3a, c, e). Corresponding results were observed at the whole plant level (Fig. 3b, d, f). In the larch soil N+ condition, the accumulation ratios of root C, shoot C, leaf N, shoot P and root P as well as the accumulation ratios of C, N and P of whole individuals of *L. olgensis* were significantly higher in the mixed culture (MN) compared with the monoculture (PN), while the whole plant P accumulation ratio of *L. kaempferi* tended to decrease more in the mixed culture (MN) (Fig. 3). There were tendencies that C, N and P accumulation ratios were higher in the mixed-forest soil (Fig. 3).

3.4. Non-structural carbohydrate pool sizes and accumulation dynamics

Different factors (competition, N fertilization and species) alone as well as their interactive effects influenced starch, soluble sugar and TNC contents of plant organs as well as those of whole plants (Tables S3, S5 and S6 in Appendix). The species benefiting from the presence of another species when growing in different types of soil tended to have higher non-structural carbohydrate contents (Tables S3 and S5).

In the larch soil N- condition, the contents of starch (roots and shoots), root soluble sugars and TNC (roots and shoots), as well as those of whole plants of *L. olgensis* became significantly higher in the mixed culture (M) compared with the monoculture (Mo) (Fig. 4). Under N fertilization in the larch soil, contents of starch (roots, shoots and whole plant), soluble sugars (leaves and whole plant) and TNC (shoots, leaves and whole plant) of *L. kaempferi* were negatively affected by the presence of *L. olgensis* (Fig. 4). In the mixed-forest soil, starch (shoots, whole plant) and both soluble sugars and TNC (roots, shoots, leaves and whole plant) of *L. kaempferi* increased under the presence of *L. olgensis*, while the contents of root soluble sugars in *L. olgensi* decreased under the presence of *L. kaempferi* (Fig. 4). There were also tendencies that the starch, soluble sugars and TNC accumulation ratios were higher in the mixed-forest soil (Fig. 4).

4. Discussion

Ecologists have suggested that both negative and positive competition play important roles in the structuring of populations and communities in the nature (Bertness and Callaway, 1994; Trinder et al., 2013; Biswas and Wagner, 2014). Through different experiments in diverse environments, researchers try to find explanations for how and to what extent neighboring organisms influence competition dynamics. In our study, we discovered that the soil type has an important role in determining competition relationships.

4.1. Competition dynamics responding to N fertilization

Tilman's theory (1987) suggests that competition for soil nutrients is stronger at low nutrient levels compared with high nutrient levels, while the stress gradient hypothesis (Bertness and Callaway, 1994) proposes that individuals of different species may negatively compete for resources or space in a productive environment but they may positively compete (facilitate) in a severe environment, and there is a possibility for intraspecific competition for the same resources or space (Miller, 1996; Goldenheim et al., 2008; Maestre et al., 2009; Fajardo and McIntire, 2011; Liu et al., 2013). In the productive soil (larch soil N+), *L. kaempferi* showed strong positive inter-specific competition and some negative effects on the growth of *L. olgensis* in 2014 (Fig. 1a), which partly supported the stress gradient hypothesis. Also previously, *L. kaempferi*

has been shown to exhibit early superiority that is greatly facilitated by the presence of *L. olgensis* in the larch soil N+ (total biomasses: *L. kaempferi* 74.80 g vs. *L. olgensis* 29.22 g, $P < 0.05$; Guo et al., 2016). In 2015, RCI of *L. olgensis* greatly increased and RCI of *L. kaempferi* was still higher, although slightly lower compared to the value in 2014 in the larch soil N+ (Fig. 1b). The growth of *L. olgensis* was no longer inhibited by the presence *L. kaempferi* and its biomass was significantly higher than that in monoculture in the larch soil N+ condition (Table 1), which then partly supported the Tilman's theory (1987). Therefore, our results did not fully support either of the two contrasting competition theories.

4.2. Competition dynamics responding to soil type

Our results provided evidence that the competitive performance of the two *Larix* species was different in the larch soil N- condition and in the mixed-forest soil. Many studies have proposed that the effects of the plant-soil feedback are plant species-specific and negative (Kulmatiski et al., 2008; van der Putten et al., 2013; Hendriks et al., 2015). Successive plantation cycles reduce productivity due to negative effects on soil qualities (Fox, 2000; O'Hehir and Nambiar, 2010). Starch and TNC concentrations of shoots and roots in *L. kaempferi* from monoculture in larch soil N- condition were significantly lower than those in *L. kaempferi* from monoculture in mixed-forest soil (Fig. 2d, f). Furthermore, the starch and TNC contents and accumulation ratios also showed similar patterns (Table S5; Fig. 4).

Therefore, the negative effects of larch soil on *L. kaempferi* were probably the reason that determined its negative performance in interspecific competition with *L. olgensis* in the larch soil N- condition at 2015 (Fig. 1b).

When a plant is confronted with foreign soil, root growth may be accelerated (Hendriks et al., 2015). Resource exploration has long been considered as a major mechanism determining the success of several invasive species (Levine et al., 2003). The root (including fine and coarse root) growth of *L. olgensis* was markedly inhibited by *L. kaempferi* when compared with *L. olgensis* monoculture grown in the mixed-forest soil in 2015 (Table 1). This indicated that *L. kaempferi* was a strong competitor to capture and store nutrition relative to *L. olgensis*, when they interacted in foreign soil (Fig. 2, 3), which probably increased its C fixation and simultaneously accelerated both growth and carbon storage (Fig. 4).

4.3. Temporal changes in competition

Crone (2016) stated that the effects of among-site variation and among-year variation (environmental stochasticity) are important for the population dynamics of *Pulsatilla patens*, as revealed by a 10-year demographic monitoring study. Intraspecific competition of *Alliaria petiolata* was found to show seasonal variation in both experimental and field conditions; specifically, statistically significant negative density-dependent survival during the productive summer period and positive

density-dependent survival over the severe winter period were observed (Biswas and Wagner, 2014). The temporal determinants of responses of forest tree species to climatic changes are important for forest dynamics. For example, Linares et al. (2010) suggested that the growth decline and death of *Abies pinsapo* occurred as a result of interacting effects of both competition and climate stressors acting at long- and short-term time scales. In our study, although we regularly watered the plants to meet their specific water demand, variation in climate conditions, such as the amount of rainfall, was not measured during the experiments. However, we did find temporal changes, as there were interacting effects of competition and soil qualities. Temporal variation in the competition dynamics was also detected between the larch soil N- condition and the mixed-forest soil from 2014 to 2015. Total biomasses of the two species grown together were not significantly different in 2014 (*L. kaempferi* 31.09 vs *L. olgensis* 21.00, $P > 0.05$, larch soil, Guo et al. 2016; *L. kaempferi* 21.17 vs *L. olgensis* 29.64, $P > 0.05$, mixed-forest soil, data unpublished) and their RCIs showed no differences (Fig. 1a). However, *L. olgensis* benefited from the presence of *L. kaempferi* in the larch soil N- condition, while *L. kaempferi* benefited from the presence of *L. olgensis* in the mixed-forest soil in 2015 (Figs. 1b and 5; Table 1). We concluded that soil type effects on competition show temporal variation and species may need a relatively long time to provide proof of their competitive ability.

Through our experiments, we revealed that the resource accumulation dynamics is tightly coupled with the temporal dynamics of species competition. As shown

previously, N accumulation by *Plantago lanceolata* exceeded that of *Dactylis glomerata* during the first 62 days, but, thereafter, *D. glomerata* accumulated more N, which indicated temporal variation in competitive interactions (Trinder et al., 2012a). Neighbors may affect non-structural carbohydrate concentrations, which then influence competition performance under different environmental conditions (Anderson et al., 2001; Liu et al., 2004; Duan et al., 2014). Apparently, in our study, there was temporal variation in the concentration dynamics of non-structural carbohydrates (Fig. 2). Resource (N and P) resorption making plants less dependent on the availability of nutrients is a critical strategy in nutrient conservation, especially in deciduous species. Resource resorption is affected by nutrient addition (Lü et al., 2013; Mayor et al., 2014), and nutrient residence times or resorption efficiency are different in interspecific and intraspecific competition (reviewed by Richards et al., 2010). Non-structural carbohydrates can be reallocated from foliar to other plant parts. The process of resorption may also show temporal variation and may affect competition dynamics, although we did not explored it in this study.

4.4. Storage and competition

Plants can potentially buffer environmental changes or stochasticity by using stored resources. Many reports have depicted the role of non-structural carbohydrates in determining tolerance to severe stress, like shade and drought (Myers and Kitajima, 2007; Adams et al., 2013; O'Brien et al., 2014). Stored nutrients affect plant growth

and performance (Pellicer et al., 2000; Uhde-Stone et al., 2003; Jordan et al., 2012, 2014). Pellicer et al. (2000) suggested that the rooting of leafy cuttings of *Larix* × *eurolepis* was limited by the initial amount of N reserves. In our study, the benefiting species possessed a higher amount of nutrients and non-structural carbohydrates, as well as a stronger C accumulation compared to its neighbors. Probably our results partly answered, why some mixed cultures were more resistant to disturbances than monocultures.

Plant species are thought to have a high year-round content of non-structural carbohydrates regardless of seasonal fluctuations, habitat and climate (Hoch et al., 2003; Körner, 2003; Würth et al., 2005). Carbohydrate pools stored in aboveground parts of mature deciduous trees are estimated to be sufficient to replace the entire leaf canopy four times in the absence of photosynthesis (Hoch et al., 2003). However, a considerable fraction of the starch pool stored in the xylem becomes sequestered (Millard et al., 2007) and fails to be used (Sala et al., 2010). Although *L. kaempferi* exhibited the highest contents of starch and soluble sugar when planted with *L. olgensis* in the larch soil N+ condition in 2014, we observed that the RCI of *L. kaempferi* declined along with the increasing RCI of *L. olgensis* in 2015 when growing in the larch soil N+ condition (Fig. 1b). Consequently, the element (C, N and P) and non-structural carbohydrate accumulation ratios of *L. kaempferi* were significantly influenced by competition with *L. olgensis* in the larch soil N+ condition (Figs. 3 and 4).

4.5. Competition and temporal niche

Competition interactions are always regulated by resource partitioning, such as preferences for different nutrient forms in soil (McKane et al., 2002; Turner, 2008; Ahmad-Ramli et al., 2013). The preference for P forms regulates the competitive outcomes between *Vaccinium vitis-idaea* and *Deschampsia cespitosa* (Ahmad-Ramli et al., 2013). As shown previously, the two studied *Larix* species have different growth traits; for example, the net photosynthesis rate and content of non-structural carbohydrates of *L. kaempferi* are significantly higher than those of *L. olgensis* in normal conditions (Li et al., 2016). Differences in carbohydrate storage can explain species coexistence (Myers and Kitajima, 2007). Temporal changes in plant traits, such as root biomass and starch content of *L. olgensis* from 2014 to 2015 in two types of soil led to changes in resource competition. Resource competition is dependent on the spatial and temporal distribution of resources between species (Alpert et al., 2000). Soil reduces establishment and growth for some species, while other plant species are less harmed. Species are probably different in their demands, and there may be temporal niche differentiation. In *Larix*, competition dynamics is evidently regulated by the combined effects of species, soil type and temporal variation, which contribute to the coexistence of species and to the dynamics of their communities.

5. Conclusions

Our study revealed the effects of soil type on the competition dynamics of the two *Larix* species. N fertilization was found to be an effective method for promoting the productivity of *Larix* plantations. The results indicated that N fertilization alleviated the negative effects of *L. kaempferi* soil on the growth of *L. kaempferi* and promoted the growth of both species when they were grown in a mixed culture.

Author Contribution Statement Qingxue Guo had the main responsibility for data collection, analysis and writing, Yuanbin Zhang had a significant contribution to data collection and analysis, Danlin Wang and Yunxiang Zhang had significant contributions to data collection and experimental arrangements, Helena Korpelainen had a significant contribution to the interpretation of data and manuscript preparation, and Chunyang Li (the corresponding author) had the overall responsibility for experimental design and project management.

Acknowledgements This work was supported by the Talent Program of Hangzhou Normal University (2016QDL020). We are very grateful to the Qingyuan Experimental Station, Institute of Applied Ecology, Chinese Academy of Sciences for providing experimental sites and support.

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Table 1. Biomass (mean ± SE) of *L. kaempferi* and *L. olgensis* under different treatments in 2015.

Species		Branch (g)	Stem (g)	Leaf (g)	Shoot (g)	Coarse root (g)	Fine root (g)	Root (g)	Total (g)
L.	M	34.31(1.74)e ***	24.64(1.70)f ***	32.41(2.56)de ***	58.95(2.68)g ***	12.98(1.01)e ns	8.17(0.47)h **	21.15(1.45)e *	112.51(4.94)e ***
kaempferi		**58.41(4.32)A**	**39.17(2.20)**	**58.17(2.52)A**	**97.58(6.41)B**	**16.62(1.37)C**	**10.36(0.37)D**	**26.98(1.33)CD**	**182.73(9.85)BC**
	Mo	35.41(1.32)e ns	29.62(2.66)ef ns	32.75(2.56)de **	65.03(2.11)fg ns	13.85(1.28)e ns	7.92(0.97)h ns	21.77(1.90)e ns	119.55(3.56)e *
		41.35(2.32)B	**32.33(1.34)**	**44.97(2.09)B**	**73.68(2.84)C**	**14.47(0.72)C**	**10.08(0.59)D**	**24.55(1.29)D**	**143.20(5.70)D**
	S	67.65(1.82)b ns	54.90(3.98)a ns	57.00(2.03)b ns	122.55(2.92)b ns	23.67(0.90)bcd **	12.77(0.40)cde ns	36.43(1.24)bc ns	215.98(4.76)b ns
		67.25(3.84)A	**50.27(2.35)**	**59.36(3.06)A**	**117.52(5.65)A**	**17.92(0.86)C**	**14.00(0.50)C**	**31.92(1.13)C**	**208.81(9.60)B**
	MN	59.33(3.48)bc	44.57(1.92)bcd	39.48(0.68)cd	103.90(4.74)cd	28.76(1.39)b	14.14(0.56)abc	42.90(1.80)b	186.28(6.86)c
	PN	47.35(1.88)cd	39.44(1.47)cde	31.33(1.17)de	86.79(2.82)de	21.09(0.67)d	10.97(0.32)efg	32.06(0.99)cd	150.18(3.90)d
	SN	111.35(3.61)a	53.77(1.71)ab	89.08(3.56)a	165.12(4.68)a	37.64(0.79)a	13.67(0.34)abc	51.31(0.46)a	305.51(8.28)a
L.	M	39.97(1.53)de ns	37.80(1.57)de ns	35.52(2.20)d ns	77.78(2.22)ef ns	23.16(1.30)cd *	10.80(0.56)fg **	33.95(1.77)cd ns	147.25(4.84)d ns
olgensis		**44.61(3.27)B**	**40.72(1.47)**	**35.20(1.66)B**	**85.33(4.67)BC**	**17.65(0.89)C**	**14.79(0.75)C**	**32.44(1.61)C**	**152.97(7.39)CD**
	Mo	26.96 (1.58)f ***	32.90(2.55)ef ns	23.24(1.66)e *	59.86(3.78)g ***	18.76(0.47)d ***	10.06(0.34)gh ***	28.82(0.62)d ***	111.91(5.66)e ***
		45.71(1.78)B	**38.78(1.13)**	**35.58(3.38)B**	**84.49(2.62)BC**	**24.66(0.61)B**	**24.37(0.98)B**	**49.03(1.52)B**	**169.10(6.08)CD**
	S	54.89(2.20)bc ns	43.36(2.32)cd *	48.11(1.82)c ns	98.25(4.18)cd *	27.31(0.86)bc *	15.95(0.72)ab ***	43.26(1.57)b ***	189.62(4.87)c **
		63.81(2.77)A	**53.07(2.16)**	**58.23(4.48)A**	**116.89(4.90)A**	**35.94(1.71)A**	**40.32(1.00)A**	**76.26(2.36)A**	**251.38(11.23)A**
	MN	51.60(2.95)c	38.58(1.69)de	40.92(1.95)cd	90.18(4.33)de	26.72(0.97)bc	14.95(0.53)abc	41.68(1.23)b	172.78(5.05)cd
	PN	41.06(2.70)de	36.72(2.57)de	35.52(2.42)d	77.79(4.91)ef	27.78(1.06)bc	13.35(0.54)bcd	41.14(1.57)b	154.45(8.61)d
	SN	64.75(3.01)b	48.79(1.87)abc	59.17(2.80)b	113.55(4.78)bc	34.43(1.61)a	16.07(0.72)a	50.50(2.30)a	223.21(5.88)b
	P: F_N	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	P: F_C	0.000 **0.000**	0.000 **0.000**	0.000 **0.000**	0.000 **0.000**	0.000 **0.000**	0.000 **0.000**	0.000 **0.000**	0.000 **0.000**
	P: F_S	0.000 **0.106**	0.261 **0.020**	0.000 **0.000**	0.000 **0.852**	0.000 **0.000**	0.000 **0.000**	0.000 **0.000**	0.000 **0.067**
	P:$F_{S\times C}$	0.000 **0.019**	0.003 **0.305**	0.000 **0.007**	0.000 **0.041**	0.008 **0.000**	0.448 **0.000**	0.110 **0.000**	0.000 **0.001**

$P{:}F_{N\times C}$	0.642	0.050	0.000	0.173	0.338	0.000	0.163	0.003
$P{:}F_{N\times S}$	0.009	0.021	0.249	0.000	0.000	0.250	0.001	0.000
$P{:}F_{N\times S\times C}$	0.004	0.001	0.000	0.022	0.000	0.407	0.002	0.000

Mo, intraspecific competition; M, interspecific competition; PN, intraspecific competition under N fertilization; MN, interspecific competition under N fertilization, S, single individual, SN single individual under N fertilization. F_N, N fertilization effect; F_S, species effect; F_C, competition pattern effect; $F_{N\times S}$,N fertilization × species effect; $F_{N\times C}$, N fertilization × competition pattern effect; $F_{S\times C}$, species × competition pattern effect; $F_{N\times S\times C}$, N fertilization × species × competition pattern effect. For larch soil experiments, values followed by different lowercase letters in the same column are significantly different at $P < 0.05$ based on Tukey's *b* analysis. For mixed-forest soil experiments, values followed by different capital letters in the same column are significantly different at $P < 0.05$ based on Tukey's *b* analysis (values in bold). *** $P \leq 0.000$, ** $0.000 < P \leq 0.01$, * $0.01 < P \leq 0.05$, ^{ns} $P > 0.05$, Independent-Samples T test between two types of soil.

Figure legends

Figure 1. Relative competitive intensities (RCIs) of *L. kaempferi* and *L. olgensis* in 2014 and at 2015. (a) RCI of the two species in 2014. (b) RCI of the two species in 2015. Larch soil N- indicates *L. kaempferi* without N fertilization; larch soil N+ indicates *L. kaempferi* soil with N fertilization; mixed-forest soil indicates soil from a secondary forest. Different lowercase letters indicate significant differences between treatments according to Tukey's *b* test at $P < 0.05$. The black and white bars denote *L. kaempferi* and *L. olgensis*, respectively. For RCI calculation, please see the Methods and materials section.

Figure 2. Variation in element and nonstructural carbohydrate concentrations of *L. kaempferi* and *L. olgensis* under different treatments from 2014 to 2015. (a), (b) and (c) represent C, N and P concentration changes, respectively; (d), (e) and (f) represent starch, soluble sugar and TNC (total non-structural carbohydrates) concentration changes. Mo, intraspecific competition; M, interspecific competition; PN, intraspecific competition under N fertilization; MN, interspecific competition under N fertilization. Different lowercase letters indicate significant differences between *L. kaempferi* and *L. olgensis* in the larch soil according to Tukey's *b* test at $P < 0.05$. Different capital letters indicate significant differences between *L. kaempferi* and *L. olgensis* in the mixed-forest soil according to Tukey's *b* test at $P < 0.05$. The red dotted frame indicates treatments in the mixed-forest soil. *** $P \leq 0.000$, ** $0.000 < P$

≤ 0.01, * $0.01 < P \leq 0.05$, ns $P > 0.05$, Independent-Samples T test between the two types of soil. The bars with and without oblique lines denote *L. kaempferi* and *L. olgensis*, respectively. The white, grey and black portions denote roots, shoots and leaves, respectively.

Figure 3. C, N and P content accumulation ratios in leaves, shoots and roots as well as in the whole plant in *L. kaempferi* and *L. olgensis* under different treatments from 2014 to 2015. (a), (c) and (e) represent C, N and P content accumulation ratios in leaves, shoots and roots, respectively; (b), (d) and (f) represent C, N and P content accumulation ratios in the whole plant, respectively. Mo, intraspecific competition; M, interspecific competition; PN, intraspecific competition under N fertilization; MN, interspecific competition under N fertilization. Different lowercase letters indicate significant differences between *L. kaempferi* and *L. olgensis* in the larch soil according to Tukey's *b* test at $P < 0.05$. Different capital letters indicate significant differences between *L. kaempferi* and *L. olgensis* in the mixed-forest soil according to Tukey's *b* test at $P < 0.05$. The red dotted frame indicates treatments in the mixed-forest soil. *** $P \leq 0.000$, ** $0.000 < P \leq 0.01$, * $0.01 < P \leq 0.05$, ns $P > 0.05$, Independent-Samples T test between the two types of soil. The bars with and without oblique lines denote *L. kaempferi* and *L. olgensis*, respectively. The white, grey and black portions denote roots, shoots and leaves, respectively.

Figure 4. Non-structural carbohydrate content accumulation ratios in leaves, shoots

and roots as well as in the whole plant in *L. kaempferi* and *L. olgensis* under different treatments from 2014 to 2015. (a), (c) and (e) represent starch, soluble sugar and TNC (total non-structural carbohydrates) content accumulation ratios of leaves, shoots and roots, respectively; (b), (d) and (f) represent starch, soluble sugar and TNC content accumulation ratios of the whole plant, respectively. Mo, intraspecific competition; M, interspecific competition; PN, intraspecific competition under N fertilization; MN, interspecific competition under N fertilization. Different lowercase letters indicate significant differences between *L. kaempferi* and *L. olgensis* in the larch soil according to Tukey's *b* test at $P < 0.05$. Different capital letters indicate significant differences between *L. kaempferi* and *L. olgensis* in the mixed-forest soil according to Tukey's *b* test at $P < 0.05$. The red dotted frame indicates treatments in the mixed-forest soil. *** $P \leq 0.000$, ** $0.000 < P \leq 0.01$, * $0.01 < P \leq 0.05$, ^{ns} $P > 0.05$, Independent-Samples T test between the two types of soil. The bars with and without oblique lines denote *L. kaempferi* and *L. olgensis*, respectively. The white, grey and black portions denote roots, shoots and leaves, respectively.

Figure 1

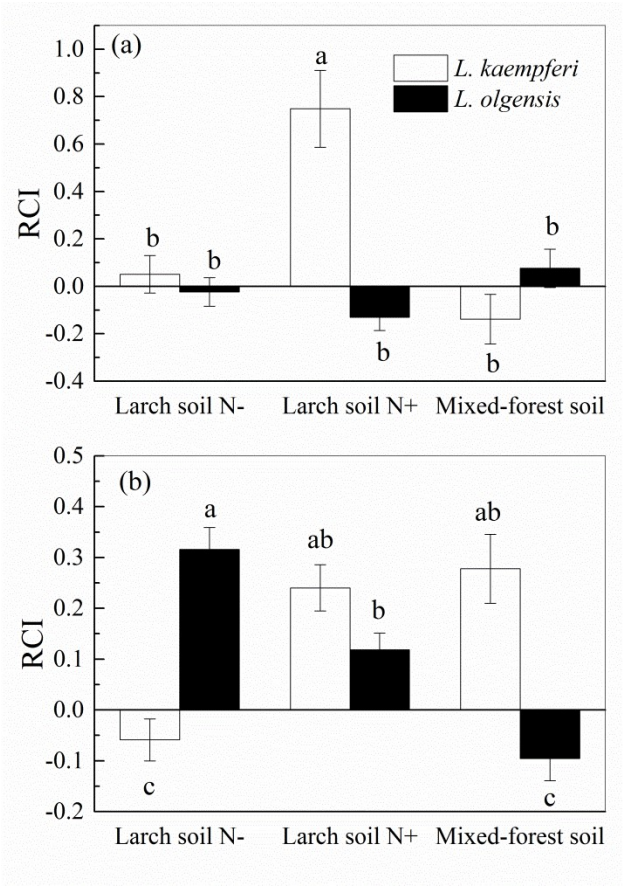

(a)
L. kaempferi
L. olgensis
RCI
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
a
b
b
b
b
b
Larch soil N-
Larch soil N+
Mixed-forest soil
(b)
RCI
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
a
ab
b
ab
c
c
Larch soil N-
Larch soil N+
Mixed-forest soil

Figure 2

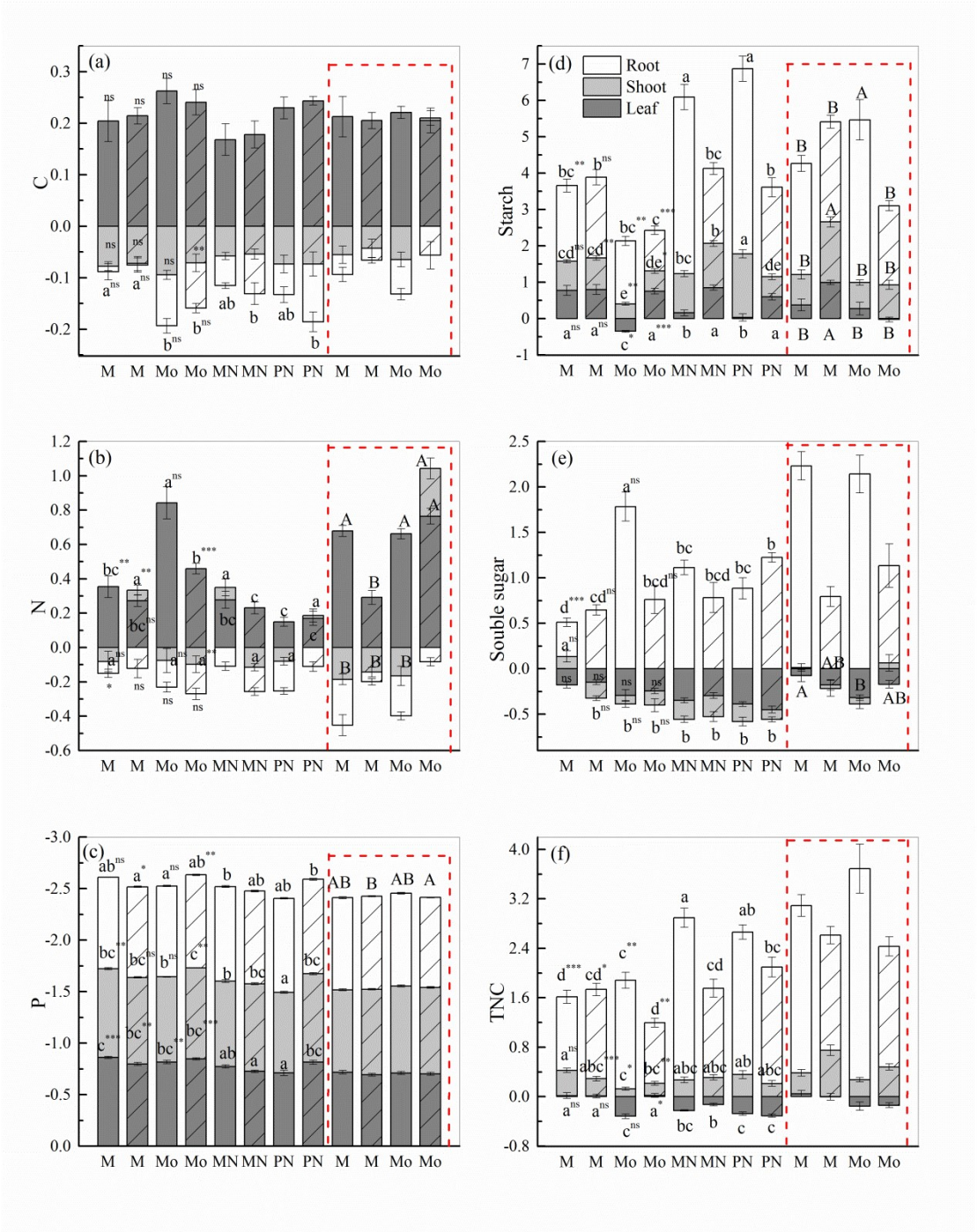

(a)
C
(b)
N
(c)
P
(d)
Root
Shoot
Leaf
Starch
(e)
Souble sugar
(f)
TNC
M M Mo Mo MN MN PN PN M M Mo Mo

Figure 3

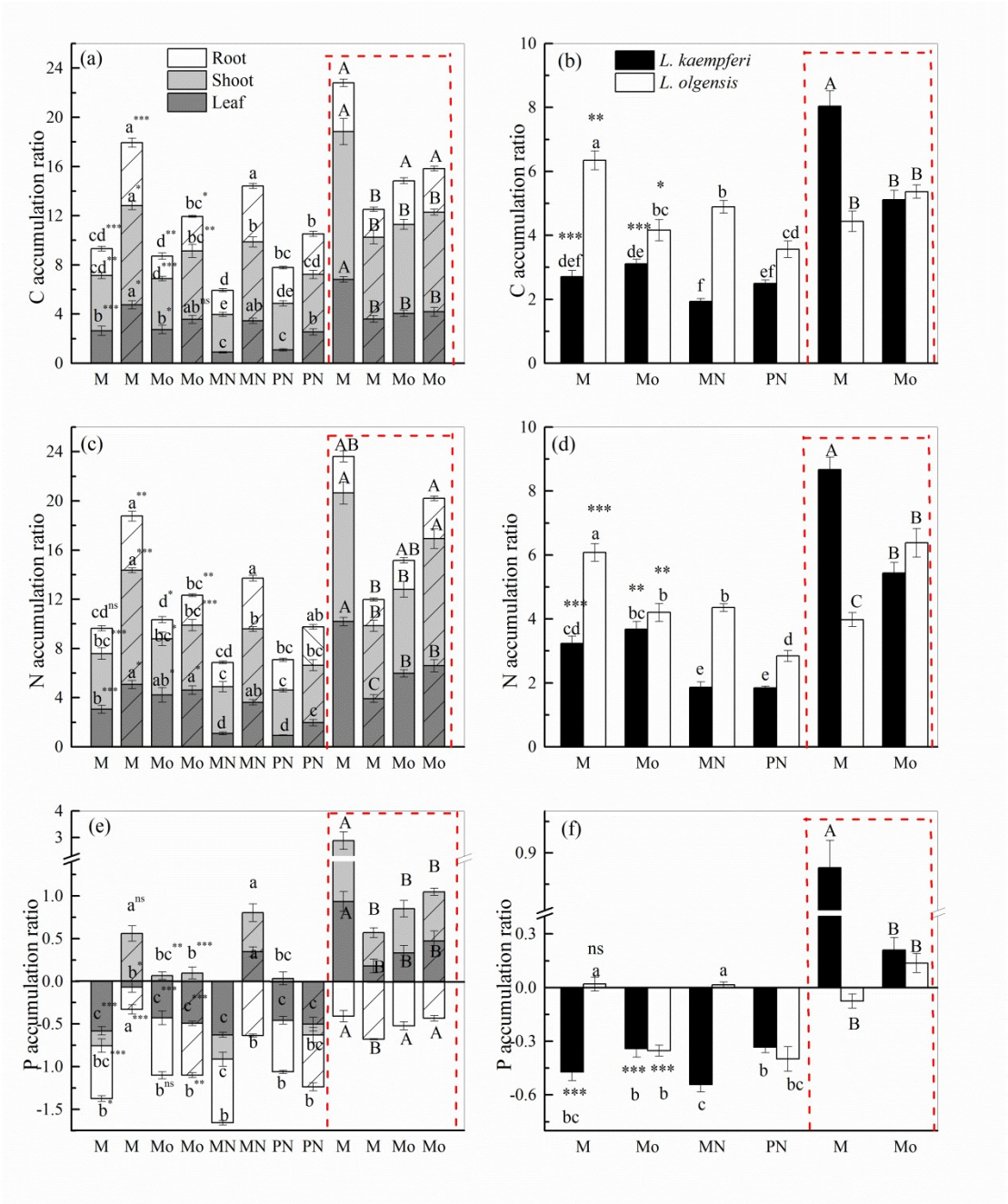
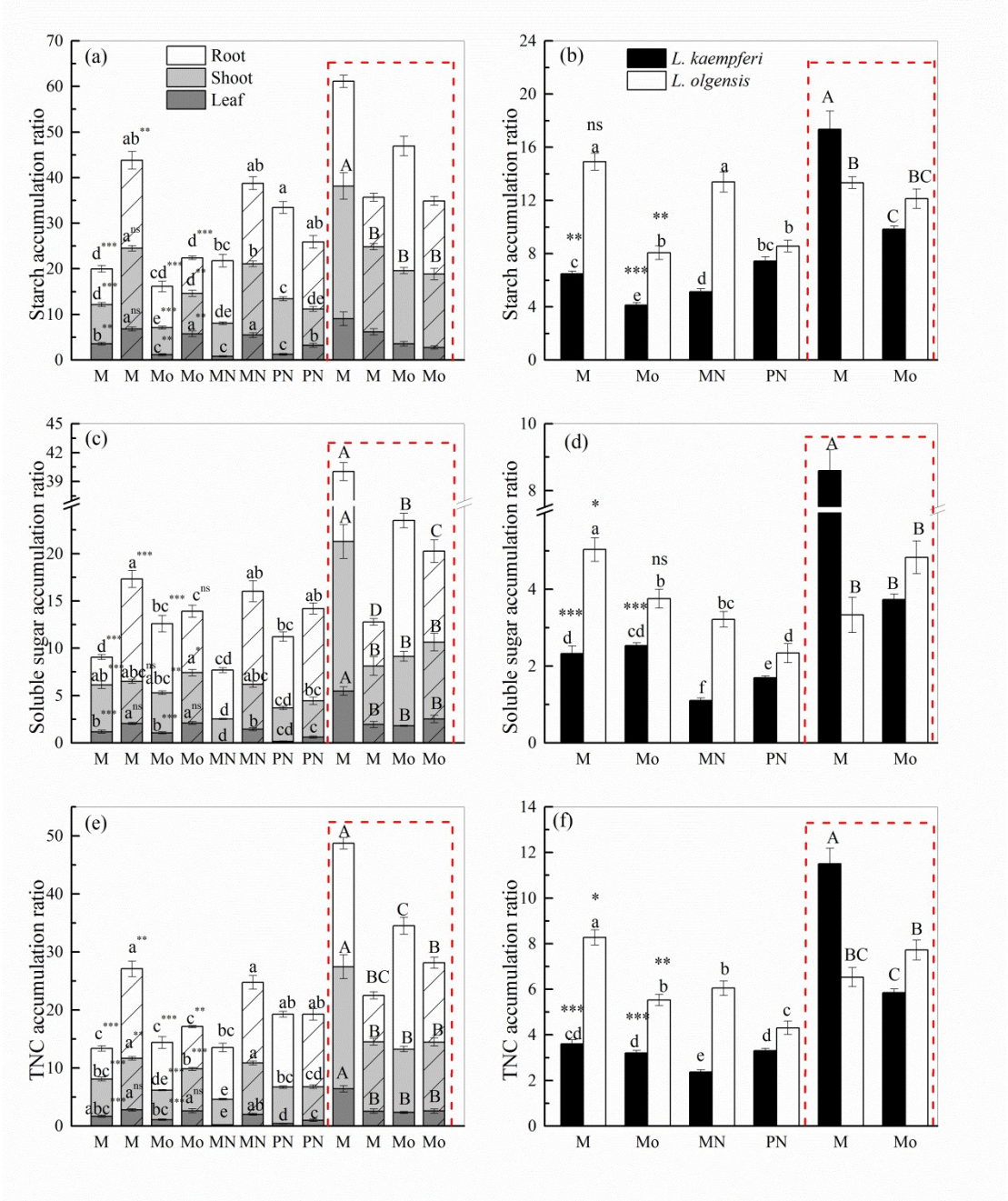

(a)
Root
Shoot
Leaf
C accumulation ratio
M M Mo Mo MN MN PN PN M M Mo Mo
(b)
L. kaempferi
L. olgensis
C accumulation ratio
M Mo MN PN M Mo
(c)
N accumulation ratio
M M Mo Mo MN MN PN PN M M Mo Mo
(d)
N accumulation ratio
M Mo MN PN M Mo
(e)
P accumulation ratio
M M Mo Mo MN MN PN PN M M Mo Mo
(f)
P accumulation ratio
M Mo MN PN M Mo

Figure 4


(a)
Root
Shoot
Leaf
Starch accumulation ratio
(b)
L. kaempferi
L. olgensis
Starch accumulation ratio
(c)
Soluble sugar accumulation ratio
(d)
Soluble sugar accumulation ratio
(e)
TNC accumulation ratio
(f)
TNC accumulation ratio
M
Mo
MN
PN