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SPECIALTY SECTION

This article was submitted to
Crop and Product Physiology,
a section of the journal
Frontiers in Plant Science

RECEIVED 29 October 2022

ACCEPTED 23 December 2022

PUBLISHED 12 January 2023

CITATION

Wu H, Zhang J,
Rodríguez-Calcerrada J, Salomón RL,
Yin D, Zhang P and Shen H (2023)
Large investment of stored nitrogen
and phosphorus in female cones is
consistent with infrequent
reproduction events of *Pinus
koraiensis*, a high value woody
oil crop in Northeast Asia.
Front. Plant Sci. 13:1084043.
doi: 10.3389/fpls.2022.1084043

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Large investment of stored nitrogen and phosphorus in female cones is consistent with infrequent reproduction events of *Pinus koraiensis*, a high value woody oil crop in Northeast Asia

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Pinus koraiensis is famous for its high-quality timber production all the way and is much more famous for its high value health-care nut oil production potential since 1990's, but the less understanding of its reproduction biology seriously hindered its nut productivity increase. Exploring the effects of reproduction on nutrient uptake, allocation and storage help to understand and modify reproduction patterns in masting species and high nut yield cultivar selection and breeding. Here, we compared seasonality in growth and in nitrogen ([N]) and phosphorus ([P]) concentrations in needles, branches and cones of reproductive (cone-bearing) and vegetative branches (having no cones) of *P. koraiensis* during a masting year. The growth of one- and two-year-old reproductive branches was significantly higher than that of vegetative branches. Needle, phloem and xylem [N] and [P] were lower in reproductive branches than in vegetative branches, although the extent and significance of the differences between branch types varied across dates. [N] and [P] in most tissues were high in spring, decreased during summer, and then recovered by the end of the growing season. Overall, [N] and [P] were highest in needles, lowest in the xylem and intermediate in the phloem. More than half of the N (73.5%) and P (51.6%) content in reproductive branches were allocated to cones. There was a positive correlation between cone number and N and P

content in needles ($R^2 = 0.64$, $R^2 = 0.73$) and twigs ($R^2 = 0.65$, $R^2 = 0.62$) of two-year-old reproductive branches. High nutrient sink strength of cones and vegetative tissues of reproductive branches suggested that customized fertilization practices can help improve crop yield in *Pinus koraiensis*.

KEYWORDS

Korean pine, strobili, branch growth, nutrient concentration, seasonal dynamics

1 Introduction

Many tree species undergo significant variations in seed production from year-to-year, a phenomenon known as masting (Kelly, 1994; Kelly and Sork, 2002; Pearse et al., 2016; Allen et al., 2017; Fernández-Martínez et al., 2019; Fernández-Martínez et al., 2020; Kelly, 2020). Inter-annual variations in seed production have been related to climatic conditions (Allen et al., 2014; Roland et al., 2014; Pearse et al., 2016; Fernández-Martínez et al., 2019; LaMontagne et al., 2020), which affect annual growth (Yasumura et al., 2006; Smith and Samach, 2013; Nakahata et al., 2021), flowering (Law et al., 2000; Cook et al., 2012), pollen availability and pollination efficiency (Koenig and Knops, 2005; Koenig et al., 2012; Pérez-Ramos et al., 2015; Pearse et al., 2016; Venner et al., 2016). In addition to climatic conditions, nutrient cycling is essential in regulating masting behaviour and reproductive mechanisms (Kelly, 1994; Kelly and Sork, 2002; Sala et al., 2012; Pearse et al., 2016; Han et al., 2017; Fernández-Martínez et al., 2019; Fernández-Martínez et al., 2020; Kelly, 2020) because reproduction consumes a significant amount of carbohydrates and mineral nutrients. Experimental evidence suggests that masting species accumulate reserves during 2-4 years for the subsequent masting reproduction event to occur (Sork et al., 1993; Yamauchi, 1996; Satake and Bjørnstad, 2008; Pearse et al., 2016). During the masting event, a significant fraction of resources is allocated to reproduction (e.g. fruit and seed development) to the detriment of growth or defense (Venner et al., 2016; Allen et al., 2017; Nakahata et al., 2021).

Korean pine (*Pinus koraiensis* S. et Z.) is a monoecious evergreen gymnosperm that naturally distributed in Northeast China, Korean Peninsula and Russia Far-east (Shen, 2003; Wang and Chen, 2004). *P. koraiensis* is a major source of timber and edible pine nuts due to its excellent wood properties and the substantial production of nutritious seeds and trees reach reproductive age at 20 - 30 years old, and female cones take two years to develop. (Shen, 2003; Wang and Chen, 2004; Xie et al., 2016; Zhang et al., 2017; Liao et al., 2021). Like many other pine species, *P. koraiensis* is a prominent masting tree, and its inter-annual periodicity is 3 to 5 years (Shen, 2003; Cheng et al.,

2017), with massive cone production during the masting year consuming a large share of carbohydrates and mineral nutrients (Han et al., 2017; Yin et al., 2019; Wu et al., 2021). *P. koraiensis* is one of the 4 major nut trees globally (Xie et al., 2016); however, compared with other orchard trees (e.g. almond or chestnut), *P. koraiensis* remains at an early stage of domestication. There is certain blindness in the management and fertilization regimes of the species, which significantly limits its economic potential.

Mineral nutrients required for plant growth, development, and reproduction are mainly taken up from the soil by the roots and transported upwards through the xylem to organs aboveground (Wiley and Helliker, 2012; Congreves, et al., 2021). Nevertheless, mineral nutrients consumed for spring growth are commonly remobilized from storage tissues rather than taken up by the roots (Han et al., 2008; Nowak-Dyjeta et al., 2017), as water and nutrient transport through the xylem is still constrained by a low evaporative demand (Millard and Grelet, 2010; El Zein et al., 2011), as observed in *Picea* and *Pseudotsuga* seedlings (Van den Driessche, 1985; Proe and Millard, 1994). The development of reproductive organs constitutes an additional resource sink that competes with growth and storage. Nitrogen (N) and phosphorus (P) are two macronutrients often limiting the growth and reproduction of masting plant species (Newbery et al., 2006; Sala et al., 2012; Ichie and Nakagawa, 2013; Han et al., 2014) which can be readily translocated from leaves and woody tissues to reproductive organs for seed maturation (Miyazaki et al., 2002; Han et al., 2011). Likewise, vegetative branches neighboring reproductive branches can also act as nutrient suppliers (Munoz et al., 1993; Miyazaki et al., 2014), a frequent behavior during masting events (Sork et al., 1993; Satake and Bjørnstad, 2008; Ichie and Nakagawa, 2013; Sala et al., 2012; Miyazaki et al., 2014). Therefore, N and P content commonly decreases during the masting event throughout tree organs (Ichie and Nakagawa, 2013; Sala et al., 2012; Miyazaki et al., 2014). Nevertheless, nutrient allocation patterns seem to be species-, organ- and nutrient-specific. For example, during the masting of *Pinus albicaulis*, N and P concentrations ([N] and [P] hereafter) were reduced compared to previous, non-masting years only in reproductive branches, while during the following year, [N]

and [P] depletion occurred in both vegetative and reproductive branches (Sala et al., 2012). In branches, stem and roots of *Dryobalanops aromatica*, [P] was reduced by more than half during reproduction compared to a non-masting year, while [N] remained stable (Ichie and Nakagawa, 2013). Therefore, a better understanding of mineral nutrient tree demand, absorption capacity and allocation during reproduction cycles will help design species-specific fertilization treatments, with the ultimate goal of shortening reproduction cycles and increasing gross seed production in the long term. In line with this, previous studies in different species have suggested that N- or P-fertilization enhances tree growth (Turner et al., 2002; Jasim, 2013), improves pollen, ovule viability and seed production (Callahan et al., 2008; Smaill et al., 2011; Ghanem et al., 2014; Bogdziewicz et al., 2017), and reduces the interval of masting events (Bogdziewicz, 2022).

This study aims to assess whether the growth of reproductive (cone-bearing) branches is inhibited by the mast event and whether cone maturation depletes nutrient availability in reproductive branches of Korean pine. To answer these questions, we monitored the seasonal dynamics of stored nutrients and the reproductive output (cone yield) in Korean pine during a masting year. Specifically, [N] and [P] seasonality in needles, twigs and cones of reproductive and vegetative branches were measured. We also examined the effect of masting on the growth of young (one- and two-year-old) branches. We hypothesize that (i) the growth of young reproductive branches will be lower than that of vegetative branches due to the diversion of nutrients and carbohydrates for reproductive purposes. Likewise, we predict (ii) stronger N and P depletion during cone maturation in vegetative tissues (needle, phloem and xylem) of reproductive branches relative to vegetative ones. We further expect (iii) the reproductive output to be inversely related to [N] and [P] in vegetative tissues at the seasonal timescale.

2 Materials and methods

2.1 Study site and sampled trees

This study was conducted at the Maoershan Research Station of the Northeast Forestry University (127°30'–127°34' E, 45°21'–45°25' N; Heilongjiang, China), in the northwest ridge of the Zhangguangcai Mountains. The area is characterized by a continental temperate monsoon climate, with warm, humid summers and cold, dry winters. The mean annual temperature is 2.8°C, and the mean temperatures in the coldest (January) and hottest (July) months are -19.6°C and 20.9°C, respectively. The growing season lasts from May to September, approximately 120 to 140 days. The mean annual precipitation is 723 mm, with 477 mm occurring from June to August. Soils are Hap-Boric Luvisols, with high organic matter content and good drainage.

More details on the site and soil characteristics can be found in Wang et al. (2006). This study was conducted during the 2018 growing season in a 5-ha *P. koraiensis* stand planted in 1968. The site is located 490–510 m above sea level and has an average slope of 15° facing the north. The mean (\pm standard error) height of the trees in 2018 was 13.5 (\pm 0.6) m, and the mean diameter at breast height was 34.0 (\pm 3.6) cm.

2.2 Sampling time and protocol

Five healthy trees with a large production of cones accessible for climbing were selected for measurements. Trees were sufficiently spaced to prevent significant shading by neighbors. For each tree, we selected five branches bearing cones (i.e. reproductive branches) and five branches with no cones (i.e. vegetative branches) from the sun-lit southwest section of the upper canopy. Selected reproductive and vegetative branches were spaced at least 2 m to avoid the influence of cones on traits of vegetative branches. One reproductive and one vegetative branch per tree were harvested five times during the 2018 growing season. In the fifth sampling time, two additional reproductive branches were sampled to better analyze the relation between cone number and end-of season nutrient status. Sampling dates were established according to the development of female cones (hereafter, cones; Figure 1): (1) before the appearance of new shoots and cone growth (May; DOYs (day of year) 128); (2) at an early stage of cone growth, when new shoots had begun to grow (June; DOYs 172); (3) at a stage of rapid cone expansion, when new shoots had stopped growing (July; DOYs 204); (4) when the cones are ripe and ready for harvesting (August; DOYs 237); (5) when the cones are fully mature, and trees are nearly dormant (September; DOYs 258).

At each sampling time, the branches were transported to the laboratory with an ice cooler. In the laboratory, the length and width of cones were measured. Foliar (needles), xylem, phloem (including bark) and cone (including seeds) tissues were manually separated to determine their dry biomass. For this, organs were oven-dried in a forced-air oven at 75°C until constant dry mass. The dried material was ground into a fine powder in a steel ball mill (Retsch MM400, German) and dry-stored until further biochemical analyses. In the last sampling date (DOYs 258), diameter and length were measured in one- and two-year-old branches.

2.3 N and P concentrations

We used an automatic Kjeldahl analyzer (model KT260; Foss Inc., Hillerod, Denmark) to determine the total [N]. A subsample of each tissue was digested in 98% H₂SO₄ (w/w) and 30% H₂O₂, using CuSO₄ and K₂SO₄ as catalysts to transform N into (NH₄)₂SO₄. Thereafter, a 40% NaOH



solution (w/v) was used to release NH_3 from $(\text{NH}_4)_2\text{SO}_4$. Finally, 1% H_3BO_3 was used to transform the released NH_3 into $(\text{NH}_4)_2\text{B}_4\text{O}_7$. A solution of 0.1 M HCl was used to titrate the content of $(\text{NH}_4)_2\text{B}_4\text{O}_7$.

We used a modified H_2O_2 - H_2SO_4 method to determine the total [P] (Rapp et al., 1999; Shen et al., 2019). We digested 0.2 g of ground material in 5 mL of 98% H_2SO_4 and 2 mL of 30% H_2O_2 at 400°C for 2–3 h. When the solution had reached 100°C, 30% H_2O_2 was added dropwise until the solution became pale yellow or colorless. The digests were diluted, filtered through Whatman 2 filter paper, and finally topped up to 50 mL with deionized water. The concentration of P in the solution was determined at 700 nm with a spectrophotometer (UV-PC01; Shimadzu Corp., Kyoto, Japan). The content of N and P in each tissue was estimated by multiplying [N] and [P] by the corresponding dry biomass of each tissue.

2.4 Statistical analysis

Linear mixed models were adjusted per surveyed dependent variable. These include biomass, [N], [P], N content, and P content in needles, phloem and xylem of one- and two-year-old twigs. Branch type (i.e. vegetative vs reproductive), harvest time and their interaction were treated as fixed factors, while the tree was considered a random factor. When significant ($P < 0.05$), *post-hoc* LSD tests were applied for multiple comparisons. One-way analysis of variance (ANOVA) was used to evaluate the effect of harvest time on cone width, length, [N], [P], N content,

and P content in reproductive branches. Finally, linear regressions between cone number and N and P content were adjusted separately for needle and twig tissues (xylem and phloem) for reproductive branches. Statistical analyses were performed using SPSS 26.0 for Windows (SPSS, Chicago, USA), and figures were plotted with SigmaPlot 10.0 (Systat Software, San Jose, USA).

3 Results

Branch type (reproductive or vegetative) and harvest time had a significant effect on [N] and [P] in needles, phloem and xylem of both one- (Figure 2) and two- (Figure 3) years-old twigs, with the interaction between branch type and harvest time being significant in most cases (Table S1). Overall, [N] and [P] in needles, phloem and xylem were lower in reproductive branches than in vegetative branches. Among tissues, [N] and [P] were generally highest in needles, lowest in the xylem, and intermediate in the phloem.

Seasonality in [N] and [P] was roughly similar across monitored tissues and for one- and two-year-old twigs (Figures 2, 3, respectively). The concentrations were highest in spring (May–June), decreased as organs matured during summer (July–August), and increased again by the end of the growing season (September), without fully recovering spring values in the case of one-year-old twigs. The only exception to this seasonal behavior was observed for [P] in needles, which increased in two-year-old twigs as the growing season progressed. The

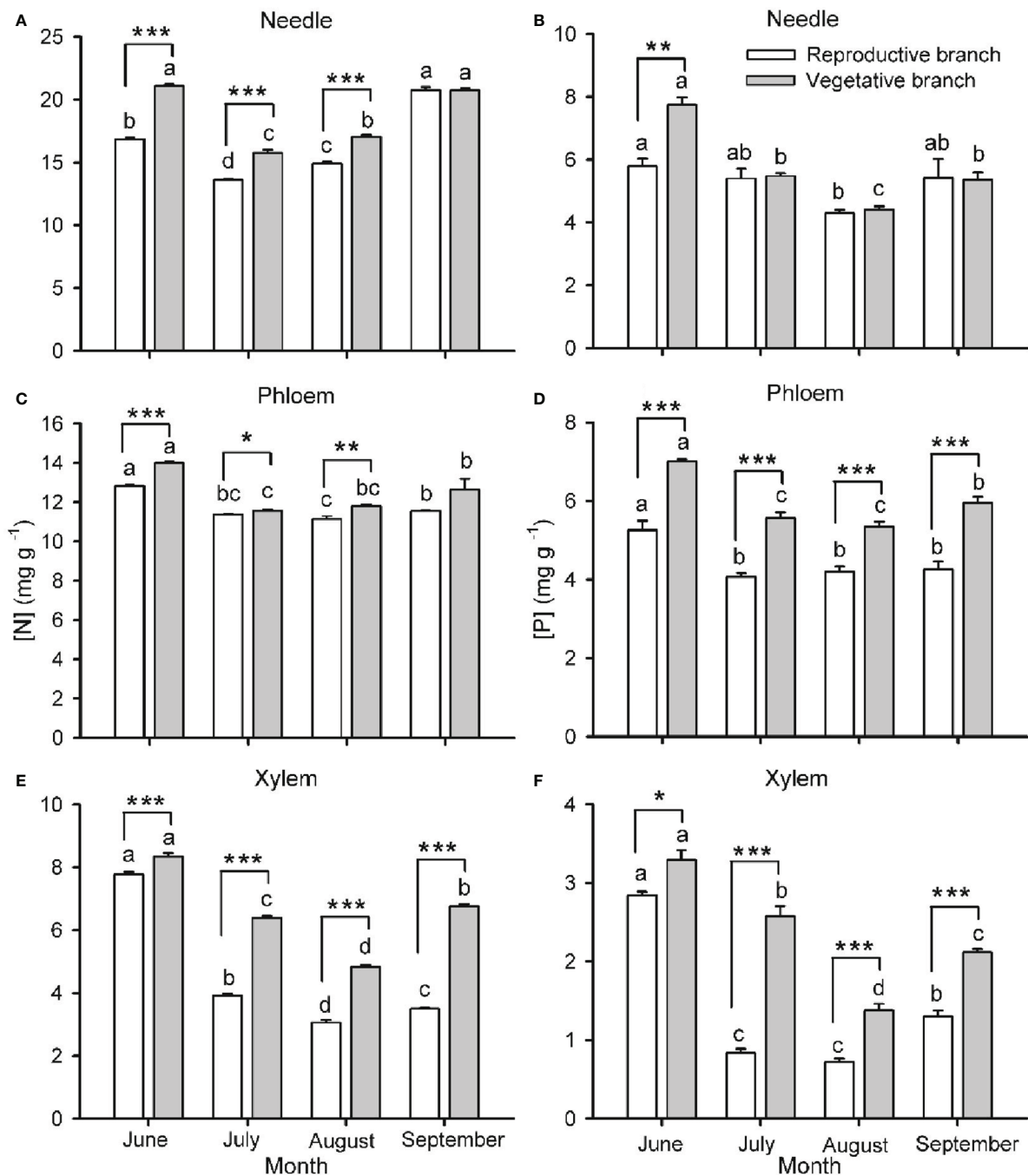


FIGURE 2 Nitrogen ([N]; A, C, E) and phosphorus ([P]; B, D, F) concentrations in needles (A, B), phloem (C, D) and xylem (E, F) of one-year-old twigs of *Pinus koraiensis* during four sampling times (June, July, August and September, corresponding to DOYs 172, 204, 237 and 258, respectively). Bars and arrows represent the mean and corresponding standard error from five trees, respectively. Asterisks indicate significant differences between branch types for a given harvest time; *, ** and *** indicate significance levels at $P < 0.05$, 0.01 and 0.001, respectively. Different lowercase letters indicate significant differences between harvest times for a given branch type.

seasonality of [N] and [P] was different in reproductive and vegetative branches. For one-year-old twigs, differences in needle [N] and [P] between branch types were higher during early summer than in September, while differences in xylem [N] and

[P] were higher in September than in June (Figure 2). For two-year-old twigs, xylem and phloem [N] were higher in September than May in vegetative branches and lower in May than September in reproductive branches. Similarly, xylem [P]

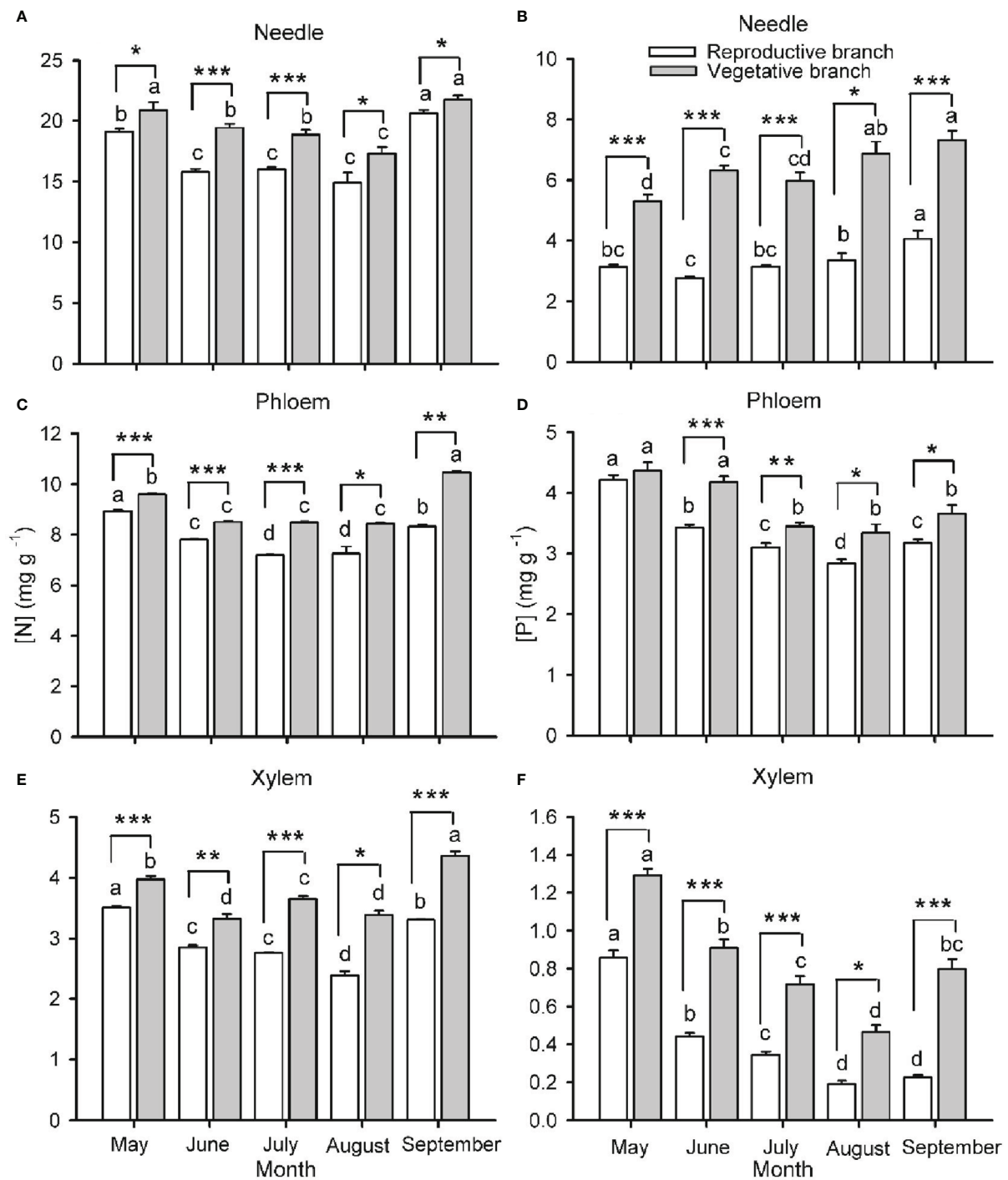


FIGURE 3 Nitrogen ([N]; A, C, E) and phosphorus ([P]; B, D, F) concentrations in needles (A, B), phloem (C, D) and xylem (E, F) in two-year-old twigs of *Pinus koraiensis* at five sampling times (May, June, July, August and September, corresponding to DOYs 128, 172, 204, 237 and 258, respectively). Bars and arrows represent the mean and corresponding standard error from five trees, respectively. Asterisks indicate significant differences between branch types for a given harvest time; *, ** and *** indicate significance levels at $P < 0.05$, 0.01 and 0.001, respectively. Different lowercase letters indicate significant differences between harvest times for a given branch type.

recovery in September was higher in vegetative than in reproductive branches (Figure 3).

Branch type, harvest time and their interaction had a significant effect on the biomass of needles, phloem and xylem of one-year-old twigs, while these effects were tissue-specific on the biomass of two-year-old twigs (Table S1; Figure 4). The biomass of all tissues of one- and two-year-old reproductive branches was significantly higher than those of vegetative branches during late-summer (August and/or September), but not in spring (May) except for xylem biomass of two-year-old twigs. In two-year-old twigs of vegetative branches, needle and phloem biomass decreased significantly from spring to summer. The width, length, and biomass of individual cones increased over time from May to August, when growth ceased (Figure 5). Cone [N] was highest in May (ca. 24.3 mg g dw⁻¹), then decreased significantly in June, and maintained a similar concentration throughout its developmental period after a slight recovery in July (ca. 21.1 mg g dw⁻¹). Cone [P] was also highest in May (ca. 2.8 mg g dw⁻¹) and maintained a similar concentration of 2.3 mg g dw⁻¹ after an initial drop in June.

Due to the relatively small changes in cone [N] and [P] as cones matured, N and P content in cones were primarily determined by biomass dynamics, with the lowest values in May followed by a progressive increase during the growing season (Figure 6). At the end of the growing season, in reproductive branches, approximately 73.5% and 51.6% of the N and P content were allocated into cones, 17.6% and 29.4% to needles, 5.7% and 15.3% to the phloem, and 3.2% and 3.7% into the xylem. In vegetative branches, 65.6% and 53.6% of N and P was allocated into needles, 25.8% and 37.9% into the phloem, and 8.6% and 7.5% into the xylem.

To further understand nutrient effects on cone production, the linear relationships between cone number and end-of-season twig size, N and P content of needle and twigs were explored *via* regression analysis (Figure 7). Twig length was unable to predict cone number ($R^2 < 0.01$, $P = 0.777$). By contrast, cone number was positively correlated with twig diameter, N and P content in needles and twigs of two-year-old twigs ($R^2 = 0.68, 0.64, 0.73, 0.65$ and 0.62 , respectively, all $P < 0.001$).

When evaluating the relation between cone number and needle and twig [N] and [P], cone number was positively correlated with [N] and [P] in needles and twigs of two-year-old twigs ($R^2 = 0.78, 0.90, 0.78$ and 0.31 , respectively, all $P < 0.05$) (Figure S1), indicating the wide range of [N] and [P] in twigs was a significant predictor of cone number.

4 Discussion

Large amounts of mineral nutrients and carbohydrates are consumed during a masting event (Kelly, 1994; Allen et al., 2017). The plant life-history theory holds that reproduction and vegetative growth compete for resources, so increased

reproductive effort leads to decreased vegetative growth (Wiley and Helliker, 2012). Previous studies support this theory: trees have lower secondary growth in masting than in non-masting years (Vaast et al., 2005; Han et al., 2011), and fruit-bearing branches grow less than branches without fruits (Han et al., 2011; Miyazaki, 2013). However, this is not always the case (Sala et al., 2012; Zhang and Yin, 2019). Contrary to our first hypothesis, results show that the increase in biomass over the last stage of cone maturation was significantly higher in reproductive branches than in vegetative branches (Figure 4), denoting that cone development did not limit the growth of reproductive branches. This unexpected observation may be due to two reasons. First, carbohydrates and mineral nutrients needed for cone development come from vegetative branches (Miyazaki et al., 2007; Zhang and Tanabe, 2008; Pasqualotto et al., 2019; Wu et al., 2021), reducing their carbohydrate concentrations and growth. Second, cones could be only formed in the branches storing larger amounts of resources and thus growing (and reproducing) more (Ichie et al., 2005; Yasumura et al., 2006). The latter hypothesis would explain the correlation between cone number and branch dimensions observed in a previous study (Yin et al., 2019) and between cone number and branch diameter, N and P content observed here (Figure 7). Consistent with this rationale, previous studies in *Nyssa sylvatica* (Cipollini and Stiles, 1991) and *Rhododendron lapponicum* (Karlsson, 1994) have reported higher nutrient concentrations in reproductive branches before the masting. In the long term, there may be a delayed cost of reproduction, which does not affect the vegetative growth of reproductive branches in the short term, but reduces it during the following seasons (Newell, 1991; Sánchez-Humanes et al., 2011; Sala et al., 2012). Delayed costs of masting in terms of vegetative growth have been observed in *Betula grossa* (Ishihara and Kikuzawa, 2009), *Acer barbinerve* (Zhao et al., 2019) and *P. albicaulis* (Sala et al., 2012).

Because vegetative growth and cone development overlap during the growing season, our second hypothesis anticipated that cone maturation would reduce [N] and [P] in vegetative tissues (needle, phloem and xylem) of reproductive branches to a greater extent than in vegetative ones. Accordingly, [N] and [P] in vegetative tissues of reproductive branches were significantly lower, with the only exception being needle [P] in one-year-old branches (Figure 2). A combination of the following factors are likely responsible for this observation: 1) active remobilization of N and P to cones from vegetative tissues, 2) a dilution of N and P as reproductive branches grow bigger (than vegetative branches) and, finally, 3) competition between cones and vegetative tissues for N and P coming from the soil (Han et al., 2008; Tanentzap et al., 2012). Similarly, the high N sink strength of seeds explains N depletion in vegetative structures of fruit-bearing branches in species such as *Fagus sylvatica* and *Taxus baccata* (Han et al., 2011; Nowak-Dyjeta et al., 2017).

In line with our third hypothesis, we expected a progressive depletion of N and P in vegetative tissues as cones mature. In

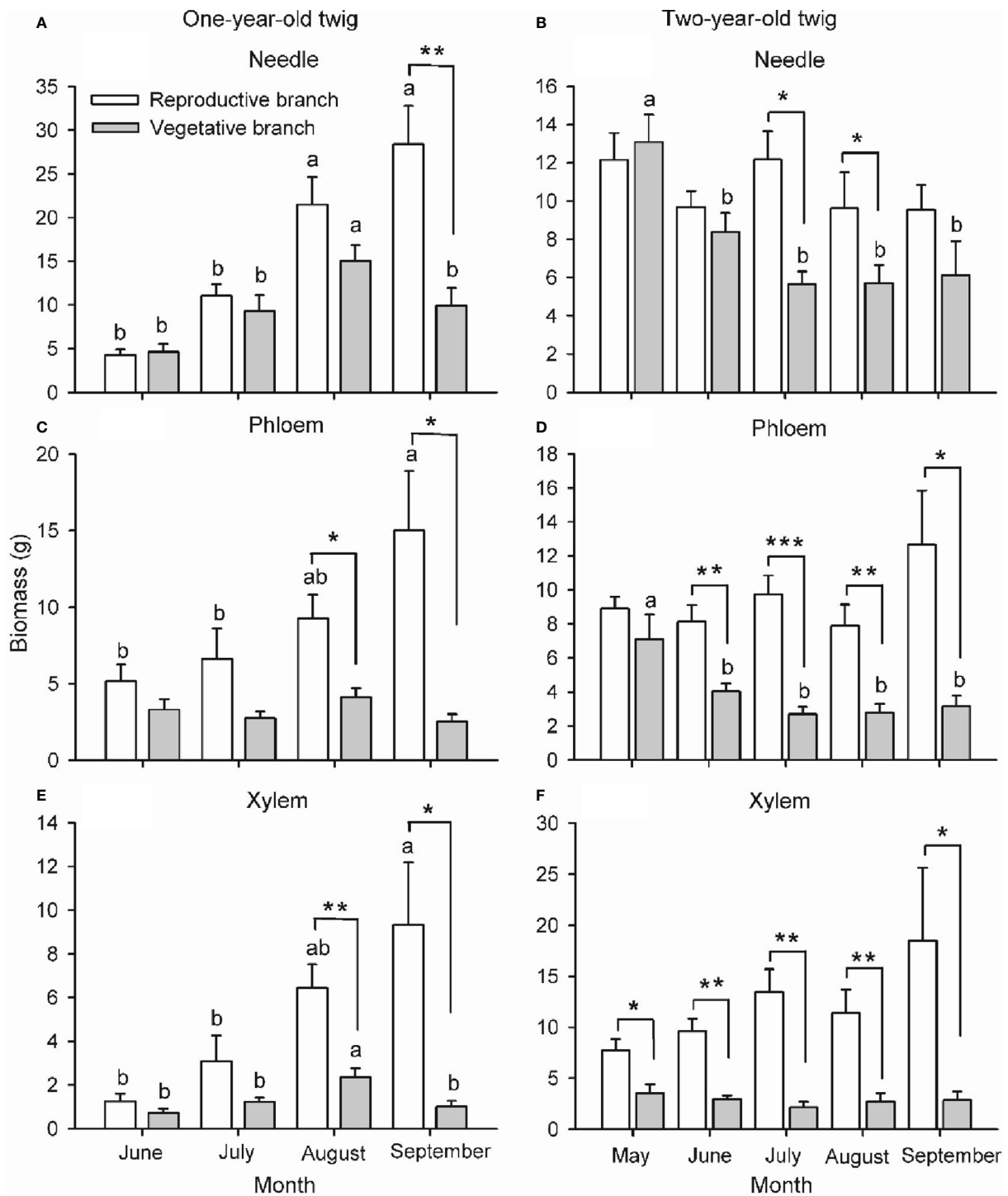
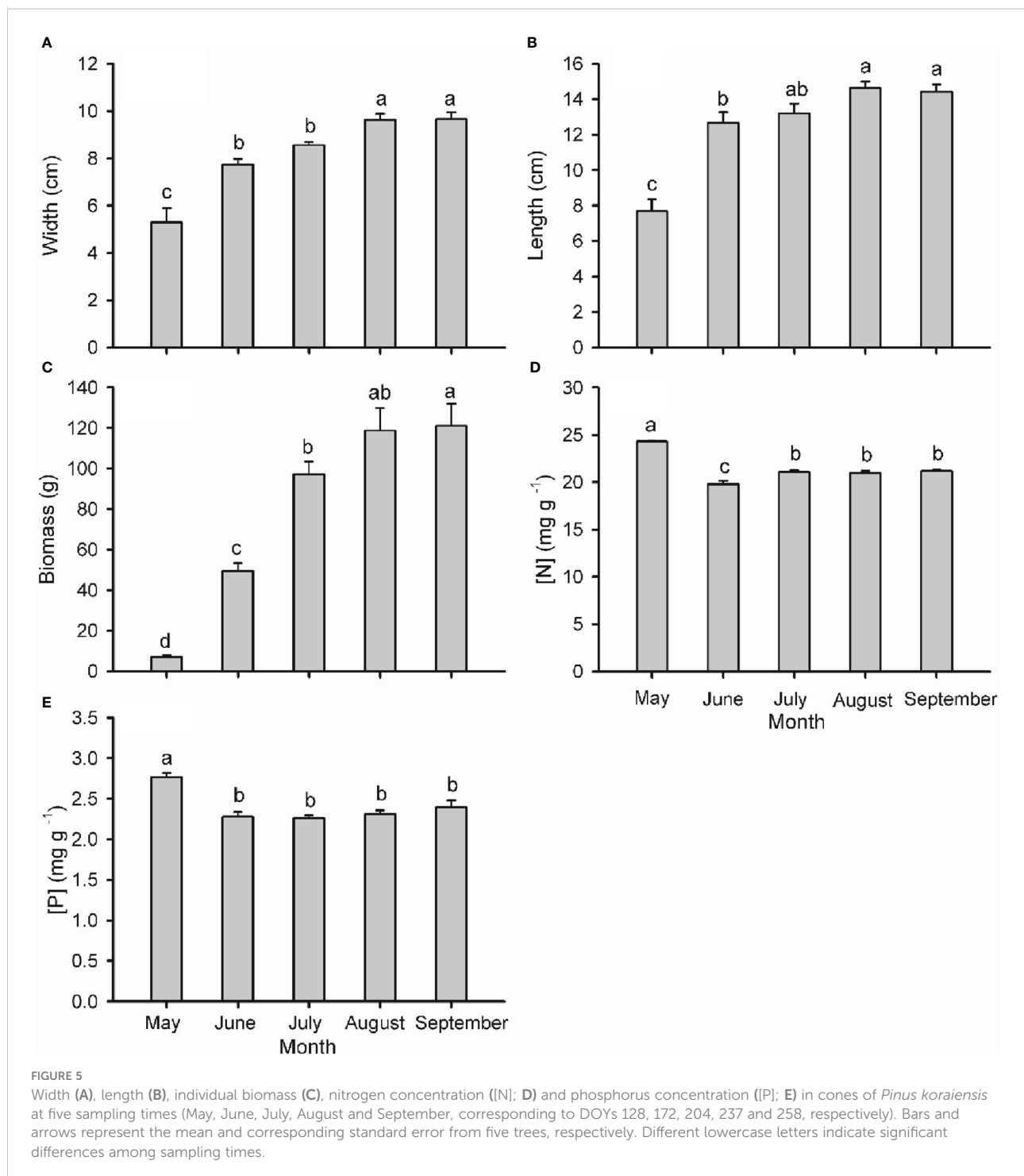
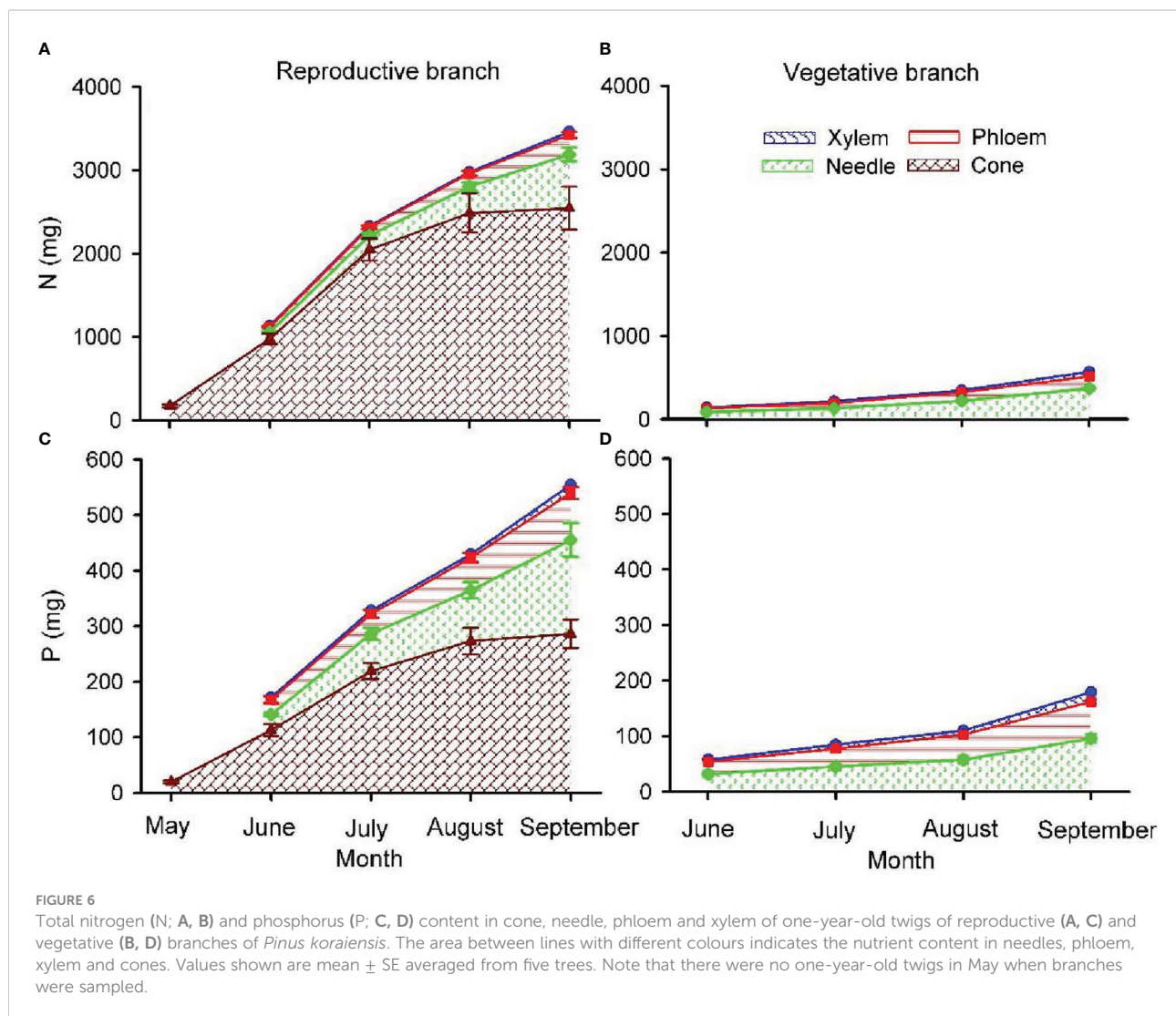


FIGURE 4
 Biomass of needle (A, B), phloem (C, D) and xylem (E, F) of one- (A, C, E) and two-year-old (B, D, F) twigs of *Pinus koraiensis* at five sampling times (May, June, July, August and September, corresponding to DOYs 128, 172, 204, 237 and 258, respectively). One-year-old twig biomass was nil in May. Bars and arrows represent the mean and corresponding standard error from five trees, respectively. Asterisks indicate significant differences between branch types for a given harvest time; *, ** and *** indicate significance levels at $P < 0.05$, 0.01 and 0.001, respectively. Different lowercase letters indicate significant differences between harvest times for a given branch type.



effect, the [N] and [P] in the phloem, xylem and needles were generally lower during mid-summer than in spring and, less so, in late summer (Figures 2, 3). The summer decline in [N] and [P] coincides with the fast shoot and cone growth, as similarly observed in *Quercus ilex* and *Q. faginea* (Silla and Escudero, 2003). These results suggest that N and P invested in shoot and cone growth exceed their root uptake rate, so N and P are being

depleted at this time (Dickson, 1989; Han et al., 2008; Nowak-Dyjeta et al., 2017). At the end of the growing season, when the nutrient demand relaxes, N and P pools are expected to replenish. Deciduous species tend to store nutrients in the branches (Tian et al., 2003), trunk (Cooke and Weih, 2005) and roots (Millard and Grelet, 2010), while evergreen species such as Korean pine primarily store nutrients in the foliage and



branches (Nambiar and Fife, 1987; Millard et al., 2001; Rodríguez-Calcerrada et al., 2012). Consistently, when cones were mature, and branches had stopped growing in the last sampling date during late summer, [N] and [P] tended to recover in the phloem, xylem and needles, with more marked increases in vegetative branches (Figure 3), where the nutrient sink strength for reproductive purposes is absent. Moreover, the complete recovery of end-of-season [N] and [P] to spring values in one-year-old needles (in contrast to the xylem) suggests that current-year xylem replaces the needles in supplying the cones with N and P during maturation (Figure 2).

Nitrogen and P are essential components of proteins and nucleic acids required by reproductive organs, which underlies growing evidence showing that N and P depletion after a masting year prevents reproduction during subsequent years (Sala et al., 2012; Han et al., 2014; Yin et al., 2019; Wu et al., 2022). The preferential allocation of nutrients to cone development and seed ripening in one-year-old reproductive branches was evidenced in

Figure 6: cone N and P content at the end of the growing season accounted for 73.5% and 51.6% of the total nutrient content of current-year branches, respectively. The progressive increase in N and P content was related to a parallel increase in cone size, while [N] and [P] were relatively constant as cones developed. Only in spring (first sampling date), before the initial, fast increase in cone size, were [N] and [P] significantly higher than in the rest of sampling dates. This observation reflects a constant, significant mobilization of nutrients from the soil and storage organs to cones to maintain a stable nutrient status (Nowak-Dyjeta et al., 2017; Wu et al., 2022). Reproductive structures are also nutrient-enriched relative to vegetative biomass in other tree species such as *F. sylvatica* (Han et al., 2011), *Q. ilex* and *Q. faginea* (Alla et al., 2012), and *P. albicaulis* (Sala et al., 2012). Compared to cones, poorer N and P allocation to needles and twig phloem and xylem might hinder flower bud primordial development in subsequent years, as reported in *Fagus crenata* (Han et al., 2008) and *P. albicaulis* (Sala et al., 2012). The branches require a period of

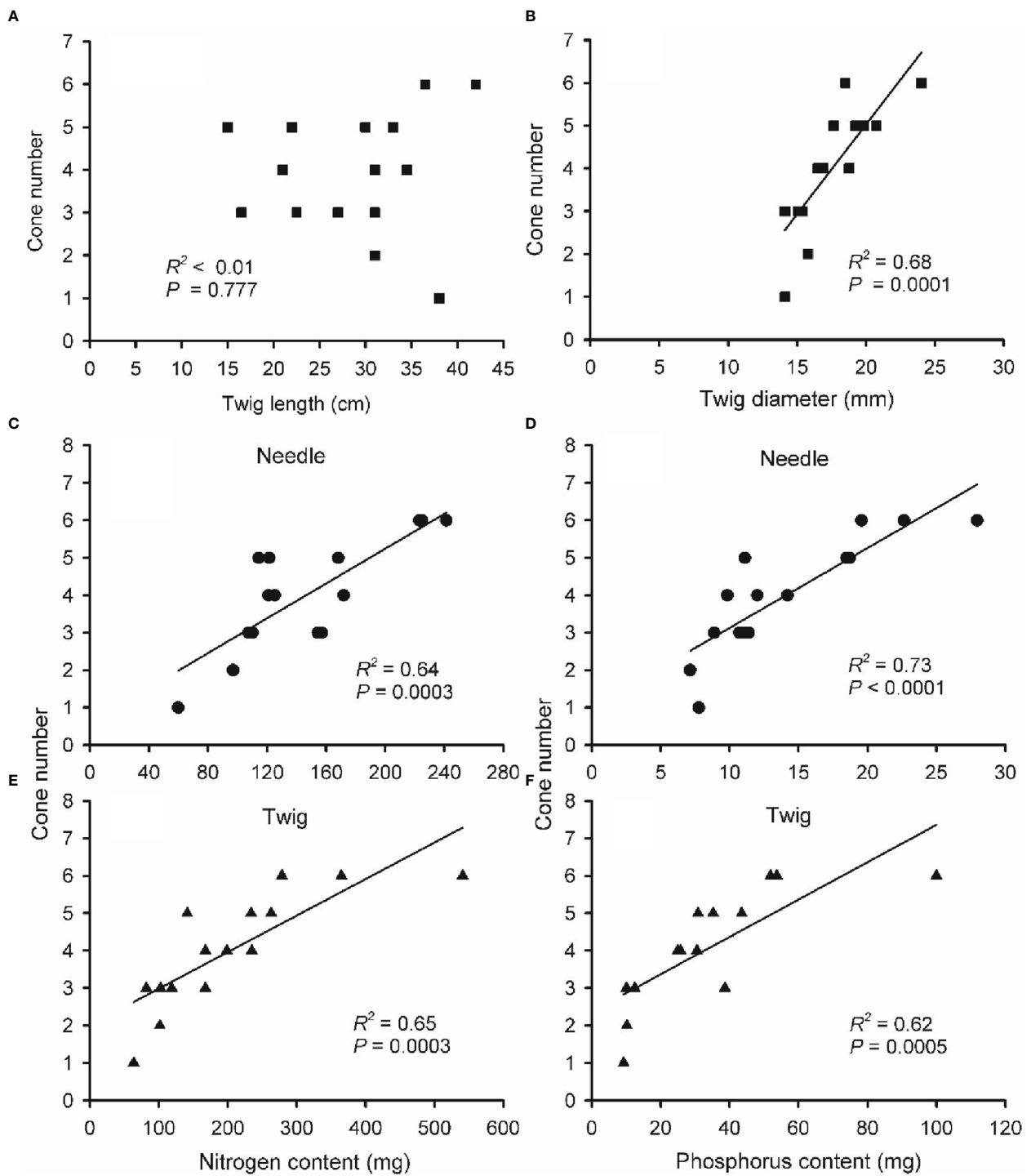


FIGURE 7
 The relationship between cone number and twig length (A), twig diameter (B), nitrogen (N; C, E) and phosphorus (P; D, F) content in needles (C, D) and twigs (E, F) of two-year-old reproductive branches of *Pinus koraiensis*. Data of cone number, twig size, N and P content were obtained from the last sampling campaign (September; five trees x three twigs). Note that some panels show less than 15 points due to overlaying data. Note the different scales for x-axes among panels.

replenishment of nutrients after the mast event, which is consistent with rare reproductive events of *P. koraiensis* (Smaill et al., 2011; Sala et al., 2012). Taken together, our results denote that the cone yield of Korean pine would substantially benefit from species-specific designs of fertilization procedures.

5 Conclusions

The results of this study evidence that cone growth occurs at the expense of nutrients primarily stored in needles and twigs of reproductive branches of *P. koraiensis*. Needle, phloem and xylem [N] and [P] in one- and two-year-old twigs of reproductive branches were lower than those of vegetative branches. However, twig growth was higher in reproductive than in vegetative branches, suggesting that more vigorous branches tend to produce a larger amount of cones. In fact, the number of cones increased with increasing diameter, N and P content of reproductive branches, with more than half of the N and P in reproductive branches being allocated to the cones. These results suggest that cone development demands a high nutrient cost. Thus, nutrients may need to cumulate to certain levels before another mast event occurs. These results can guide rational fertilization of *P. koraiensis* plantations. Further studies should test whether periodic fertilization promotes nutrient storage and reduces the intervals between masting events.

Data availability statement

The data analyzed in this study is subject to the following licenses/restrictions: The experimental data used in the study are available from the corresponding author on reasonable request. Requests to access these datasets should be directed to Hailong Shen shenhl-cf@nefu.edu.cn.

Author contributions

All authors contributed to the study conception and design. PZ and HS conceived and designed the study. DY and JZ collected

plant materials and data collection. HW, DY and JR-C analyzed the results for experiments. HW, RS, JR-C and DY contributed to the writing of the manuscript and data analyses. PZ, HS, DY, JR-C and RS revised the manuscript. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by the National Key Research and Development Program of China (Grant No. 2022YFD2201002); the Key Research and Development Program in Heilongjiang Province (Grant No. GA21B005); HW acknowledges funding from China Scholarship Council (CSC number 201906600024); and RS acknowledges funding from the Spanish Ministry of Science, Innovation and Universities (Juan de la Cierva Programme, grant IJC2018-036123-I).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2022.1084043/full#supplementary-material>

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