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# The effects of stump size and within-gap position on sprout non-structural carbohydrates concentrations and regeneration in forest gaps vary among species with different shade tolerances

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## Abstract

**Background:** To restore secondary forests (major forest resources worldwide), it is essential to accelerate the natural regeneration of dominant trees by altering micro-environments. Forest gaps are products of various disturbances, ranging from natural storms or wildfires to anthropogenic events like logging and slashing-and-burning, and sprouts of most tree species with non-structural carbohydrates (NSCs) storage can regenerate from stumps after gap formation. However, how the stump sprouts with diverse NSCs storages and stump sizes (i.e., diameters) adapt to various micro-environments of within-gap positions remains unclear. Therefore in this study, we monitored the stump sprout regeneration (density, survival, and growth) and NSCs concentrations of three dominant tree species with different shade tolerances and varying stump diameters at five within-gap positions for the first two consecutive years after gap formation.

**Results:** Stump diameter was positively correlated with sprout density, growth, and survival of all three tree species, but insignificantly related with sprout NSCs concentrations at the early stage after gap formation. The effect of within-gap position on sprout NSCs concentrations was different among species. After an environmental adaptation of two growing seasons, the north of gap (higher light availability and lower soil moisture habitat) was the least conducive for shade-intolerant *Quercus mongolica* to accumulate leaf NSCs, and the east of gap (shadier and drier habitat) was conducive to increasing the leaf NSCs concentrations of shade-tolerant *Tilia mandshurica*.

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**Conclusions:** Within-gap position significantly affected leaf NSCs concentrations of all three tree species, but most of the sprout growth, survival, and stem NSCs concentrations were independent of the various within-gap positions. Besides stump diameter, the NSCs stored in stump and root systems and the interspecific differences in shade tolerance also contributed more in sprout regeneration at the early stage (2 years) of gap formation. A prolonged monitoring (> 10 years) is needed to further examine the long-term effects of stump diameter and within-gap position on sprout regeneration. All of these findings could be applied to gap-based silviculture by promoting sprout regeneration of dominant tree species with different shade tolerances, which would help accelerate the restoration of temperate secondary forests.

**Keywords:** Non-structural carbohydrates, Sprout regeneration, Sprout growth, Sprout survival, Within-gap position, Stump size

## Background

Secondary forests have become main body of forest resources, accounting for 60% and 72% of the forest area in the entire world and Northeast China, respectively (Thompson and Donnelly 2018; Yan et al. 2019). However, secondary forests, which regenerated from the primary forests after natural or anthropogenic disturbances, have been degraded with the problems of stand structure (e.g., lack of dominant tree species, and simpler vertical stand structure) and declined ecosystem services (e.g., lower water conservation) (Zhu et al. 2007a; Yan et al. 2010, 2019). One critical approach for solving these problems above is to accelerate the natural regeneration of dominant tree species in secondary forests (Woo et al. 2011; Kang et al. 2012; Yan et al. 2019).

As a dominant form of small-scale disturbance in secondary forests, forest gap plays an important role in forest dynamics (Gendreau-Berthiaume and Kneeshaw 2009; Zhu et al. 2015). According to the concept of close-to-nature silviculture, emulating natural disturbance to create artificial gaps is a useful way to promote forest regeneration (Streit et al. 2009; Lu et al. 2018a, 2018b). This is because once artificial gaps are created, the micro-environments within a gap will vary with diverse within-gap positions (Ritter et al. 2005; Albanesi et al. 2008; He et al. 2012), and the natural regeneration of desired tree species within a gap would relate to the within-gap positions where they located. After gap formation in temperate secondary forest, there are two types of natural regeneration (i.e., seed regeneration and sprout regeneration) within a gap. Many previous researches have reported that within-gap position strongly affected seed regeneration process (i.e., seed rain, seed dispersal, soil seed bank, seed germination, seedling emergence, seedling establishment, and seedling/sapling growth) (Wang et al. 2017; Lu et al. 2018a, 2018c; Bujan et al. 2018; Yan et al. 2019). The studies on the sprout regeneration (i.e., sprout density, survival, and growth) mainly focus on sprout mechanisms (Zhu et al. 2007b), effects of stump traits (e.g., stump diameter) on

sprout regeneration (Wang et al. 2004), and sprout regeneration after a fire (Vesk and Westoby 2004). However, few studies pay attention to the effects of within-gap positions on sprout regeneration.

After gap formation in temperate secondary forests, many sprouts can regenerate from stumps or fallen logs and then grow quickly to occupy spaces with appropriate within-gap environment (Bellingham and Sparrow 2000; Bond and Midgley 2001). Sprout regeneration plays a critical role in restoring temperate secondary forests at the early stage of gap formation (Zhu 2002; Zhang et al. 2018). Therefore, the within-gap position with appropriate micro-environment may be beneficial to restore temperate secondary forests by promoting sprout regeneration.

Non-structural carbohydrates (NSCs), including soluble sugar, starch, and total NSC (the sum of soluble sugar and starch), are stored in plant tissues (e.g., leaves, stems, roots). NSCs are involved in plant metabolism and play an important role in plant survival and growth (Imaji and Seiwa 2010; Takahashi and Goto 2012; Zhang et al. 2013; Richardson et al. 2013). Soluble sugar forms in leaves and is transported from leaves to other tissues of a plant, while starch is considered as primary storage polysaccharide in plant (Dietze et al. 2014; Takahashi and Furuhashi 2016). Therefore, NSCs concentration is recognized as an indicator of a balance between carbon sources (i.e., photosynthesis) and sinks (i.e., growth) (Hoch et al. 2003; Dietze et al. 2014). Leaf NSCs storage, especially in deciduous trees, is transported to phloem before leaf falls and is utilized for growth in the next year (Wong et al. 2003; Dietze et al. 2014). Soluble sugar is directly used for cold tolerance, while starch accumulated late in the growing season and converted to soluble sugar during dormancy period, and then converted to starch when the dormancy ends (Dietze et al. 2014). Therefore, the storage of NSCs, especially in the stems of deciduous trees, is advantageous for survival and growth of trees under stress conditions (e.g., shade environment and cold season), and affects sprouting ability

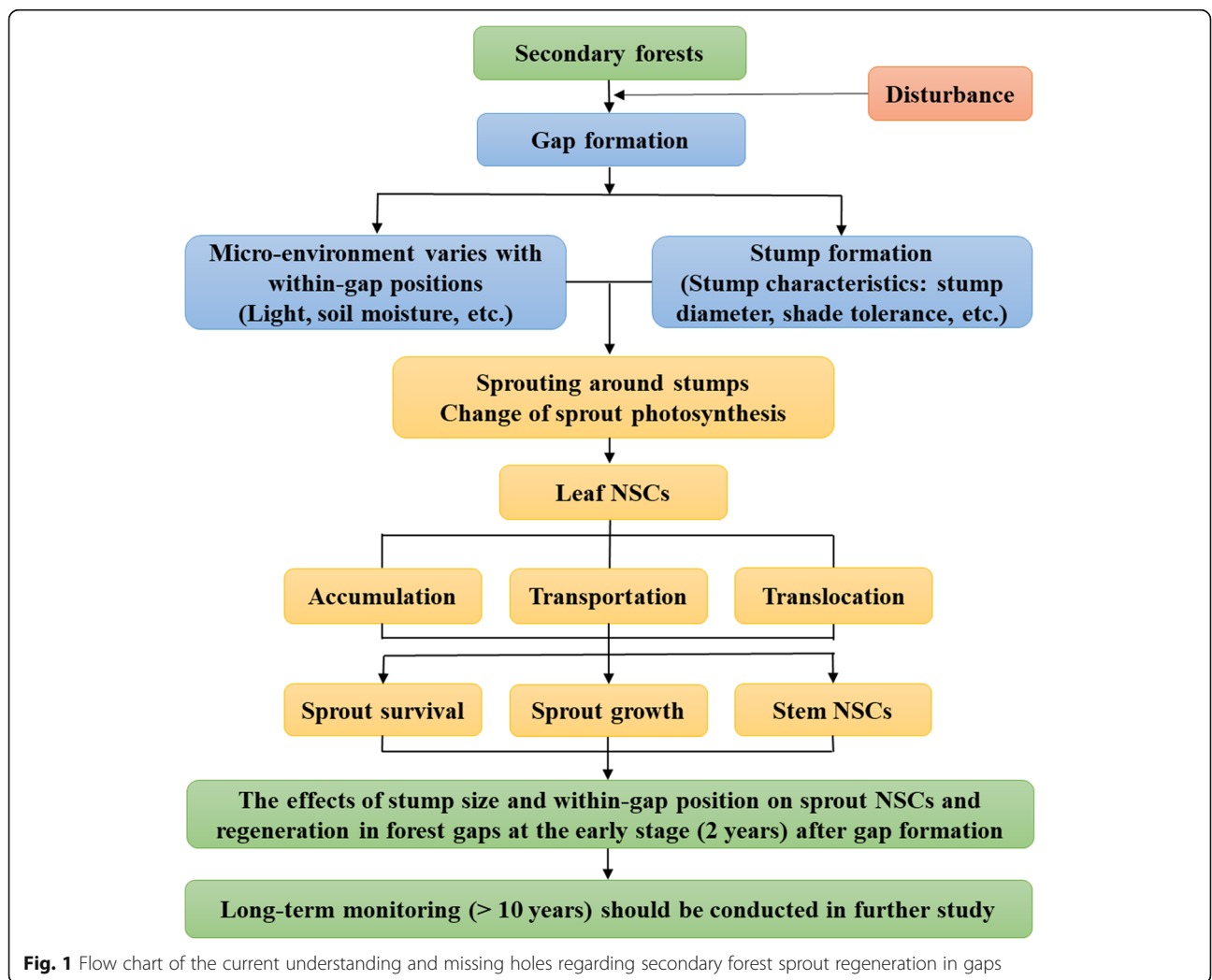
of trees after cutting or above-ground biomass loss (Latt et al. 2001; Zhang et al. 2013).

Poorter and Kitajima (2007) have indicated that it is important to focus on the changes of NSCs concentrations in relation to various environmental conditions. However, previous studies mainly focus on the seedlings originated from seed regeneration (Zhang et al. 2013) or mature trees (Wong et al. 2009; Klein et al. 2016), and little is known about the effects of diverse environments (e.g., varying within-gap positions) on sprout NSCs concentrations and consequently on sprout regeneration. Additionally, characteristics of tree residues (e.g., stump diameter) can also affect sprout regeneration, but the results vary among different tree species (Mwavu and Witkowski 2008; Knapp et al. 2017).

Here, we use a flow chart (Fig. 1) to illustrate the idea of our research, and test following hypotheses. Right after the creation of gaps, sprouting happens around stumps. Stump diameter and within-gap position can affect sprout density, growth, and survival after stump

sprouting (hypothesis 1). After sprouting, leaves start to accumulate NSCs, and the leaf NSCs concentrations will be affected by species and within-gap position (hypothesis 2). After a period of growth, assimilated carbon reallocated to other parts. Thus, the ratio of leaf NSCs to stem NSCs, and the stem NSCs concentrations will be affected by within-gap position and species (hypothesis 3).

To test these hypotheses, we conducted this work in temperate secondary forest gaps in a mountainous region of eastern Liaoning Province, Northeast China. Three dominant tree species with different shade tolerances (shade intolerant species: *Quercus mongolica* Fisch., intermediate shade tolerant species: *Acer mono* Maxim., shade tolerant species: *Tilia mandshurica* Rupr.) were selected as objects of this study. We monitored sprout survival, growth, and the NSCs concentrations in leaves and stems at five within-gap zones for the first two consecutive years after gap creation. We hope this study could provide some new insights into the gap-based silviculture by promoting sprout regeneration of



**Fig. 1** Flow chart of the current understanding and missing holes regarding secondary forest sprout regeneration in gaps

dominant tree species with different shade tolerances, which would help accelerate the restoration of temperate secondary forests.

**Methods**

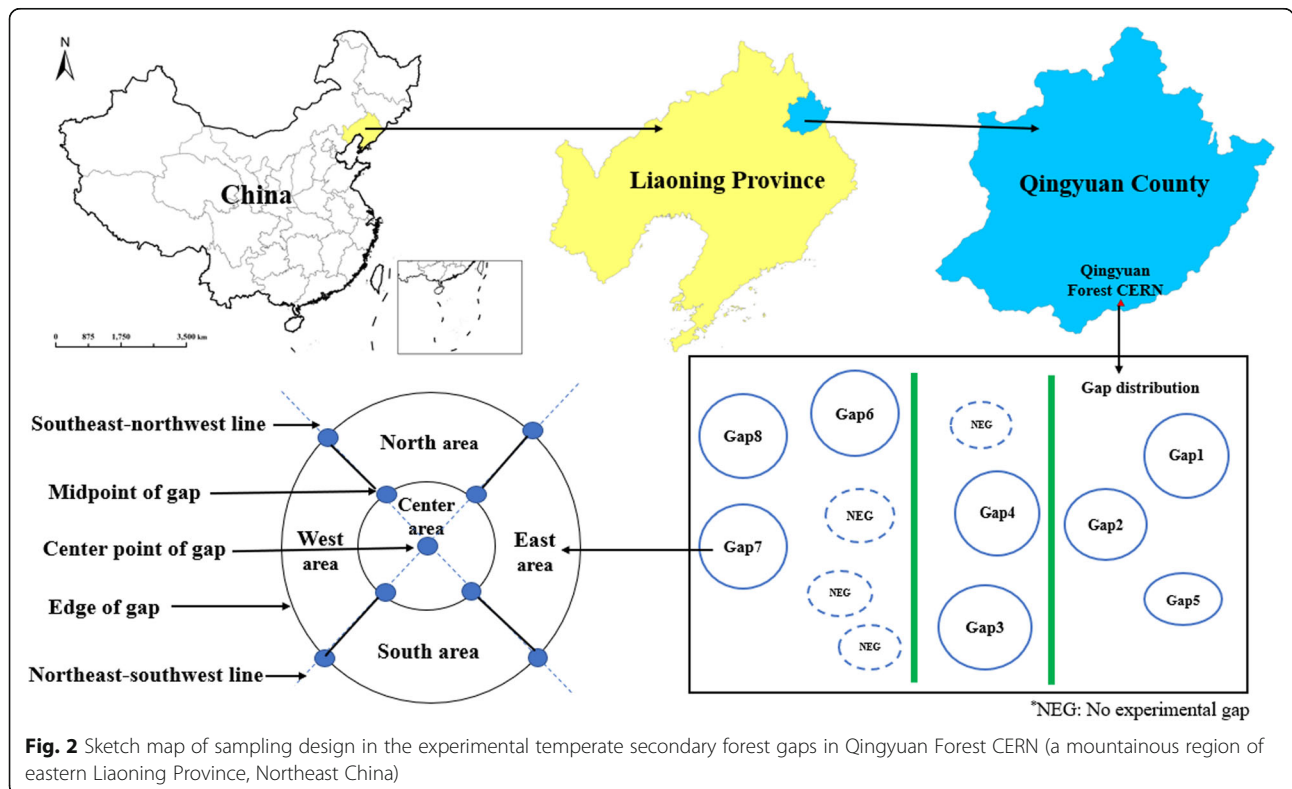
**Study site**

This study was carried out in Qingyuan Forest CERN (Chinese Ecosystem Research Network), Chinese Academy of Sciences (CAS), located in a mountainous region of eastern Liaoning Province, Northeast China (41°51'N, 124°54'E, 500–1100 m above sea level). The climate is a continental monsoon climate, with a strong windy spring, a hot and humid summer, and a dry and cold winter. The annual mean air temperature is 4.7 °C with the coldest month in January and the warmest month in July. The mean annual precipitation ranges from 700 to 850 mm, of which 80% falls during summer (from June to August). The growing season lasts from early April to late October (Yan et al. 2019; Lu et al. 2019). The soil is a typical brown forest soil consisting of 25.6% sand, 51.2% silt, and 23.2% clay (Yang et al. 2013). Historically, the study area was covered by mixed broadleaved-Korean pine forests until the 1950s. Most of the primary forests degraded over decades of exploitive timber harvesting and were completely cleared by a large fire in the early 1950s. Currently, the study area was covered by naturally regenerated secondary forests and dominated by broadleaved tree species such as *Q. mongolica*, *A.*

*mono*, *Fraxinus rhynchophylla* Hance and *Juglans manshurica* Maxim. (Lu et al. 2018c; Yan et al. 2019).

**Gap description**

Twelve artificial gaps (including eight experimental gaps and four non-experimental gaps of this study) (Fig. 2) were created on the snow-covered ground in a typical secondary forest in March 2015. The establishment of these forest gaps was served in a series of studies on the effect of forest gap on secondary forest regeneration (Lu et al. 2018a, 2018c, 2021). These forest gaps were established with different sizes referred to Zhu et al. (2015), based on the upper and lower limits of forest gaps and the actual situation of sample plots. During gap creation, all trees (including saplings) and shrubs taller than 30 cm within gaps were harvested and removed out of gaps to create a uniform forest floor only with grasses. In order to minimize the negative effects of logging on stand environments (i.e., forest soil and other canopy trees), the chainsaws instead of large harvesting machines were used to remove the logging materials. The size and shape of each experimental gap was measured using a total station (TKS-202, China), which can record the distance and direction between the center point and each border tree of gap. We used the total station to create approximately circular gaps (Lu et al. 2018c). Gap locations were randomly chosen in forests with similar site conditions, such as similar soil type, alike topography



(mountains with slope of 18–28°, slope aspect of 158–220°, and mid-slope position), similar vegetation composition, and the same history of forest management. The area of these experimental gaps ranged from 476 m<sup>2</sup> to 984 m<sup>2</sup>. The mean height and DBH (the diameter at breast height) of the border trees of all experimental gaps were 19.08 m and 29.88 cm, respectively. The basic description of experimental gaps is shown in Table 1.

### Experimental design

According to a preliminary survey of the basic information (e.g., within-gap position, tree species, sprout number per stump, stump height and diameter, sprout height and basal diameter) for all within-gap stumps at the beginning of growing season in 2015, we counted the number of stumps per tree species and took the within-gap position of stump and the shade tolerance of species into account. Finally, three dominant tree species with different shade tolerances were selected as our study objects (i.e., shade intolerant species: *Q. mongolica*, intermediate shade tolerant species: *A. mono*, and shade tolerant species: *T. mandshurica*) (Shi et al. 2006; Lu et al. 2015; Yan et al. 2016). The stumps of *Q. mongolica*, *A. mono* and *T. mandshurica* accounted for 16%, 36%, and 7% of the total number of stumps within all eight experimental gaps, respectively.

Nine points were set up in each experimental gap along four directions (i.e., southeast-center-northwest and northeast-center-southwest), of which one point located in the center of gap (i.e., center point), four points in northwestern, southeastern, northeastern, and southwestern edge of the gap (i.e., edge points), and four points in the middle of gap center point and gap edge points (i.e., midpoints) along southeast-northwest line and northeast-southwest line (Fig. 2). The center zone of gap was identified as the circular area formed by the distances from center point to midpoints. The annular area formed by the distances from midpoints to its corresponding edge points was divided into four subareas (north, south, east, and west) by the northeast-southwest

line and the southeast-northwest line. Thus, each gap was divided into five within-gap zones, including center zone (center), north zone (north), south zone (south), east zone (east), and west zone (west). The partition of five within-gap zones is shown in Fig. 2.

Three experimental stumps of each tree species in each within-gap zone were chosen for the study. Thus, we had a total of 45 stumps for the experiment (3 stumps per species for each zone × 3 species × 5 within-gap zones = 45 stumps). Three replicates of stumps for each tree species in the same within-gap zone should be chosen from different experimental gaps. To minimize the difference of sprouting ability among experimental stumps, we only chose the stump with 10–30 sprouts at the beginning of growing season in 2015. The stump height and diameter (mean ± SE) for *Q. mongolica*, *A. mono* and *T. mandshurica* were 20.38 ± 2.78 cm and 21.54 ± 3.70 cm, 21.67 ± 3.61 cm and 5.46 ± 0.63 cm, and 23.85 ± 2.91 cm and 8.96 ± 1.73 cm, respectively.

### Sprout density, survival, and growth measurement

Sprout density (the number of sprouts per stump) was examined at the beginning and the end of growing season for two growing seasons. Sprouts were considered alive when at least one green tissue was present on the stem (O'Brien et al. 2014). The sprout survival in each growing season ( $R_{e/b}$ ) was represented by the ratio of the number of sprouts per stump at the end of growing season to the number of sprouts per stump at the beginning of the same growing season.

At the end of growing season in 2015 and in 2016, we randomly selected three 1-year-old sprouts and three 2-year-old sprouts from each experimental stump, respectively, and the selected sprouts were measured and harvested for NSC analysis. The mean value of each variable of three sprouts was considered representative of the sprouts on each experimental stump. Two measurements of sprout growth characteristics (i.e., sprout height and basal diameter) were conducted. We measured the sprout height and basal diameter at the end of the growing

**Table 1** Basic description of experimental secondary forest gaps created in March 2015

Forest gaps	Gap size (m <sup>2</sup> )	Altitude (m)	Aspect (°)	Slope (°)	Height of gap border trees (m)	DBH of gap border trees (cm)	Stump number per gap
Gap1	984	678	191	22	20.0	27.3	93
Gap2	688	679	170	25	19.8	30.8	69
Gap3	968	653	195	19	17.5	28.9	67
Gap4	658	672	220	25	20.1	32.6	55
Gap5	476	664	168	18	19.4	28.8	11
Gap6	484	726	170	25	18.5	31.6	61
Gap7	512	731	158	28	17.2	26.5	101
Gap8	492	762	170	26	18.9	32.5	66

season in 2015 and 2016 for 1-year-old sprouts and 2-year-old sprouts, respectively. The sprouts were harvested and divided into leaves and stems at the end of the growing season in 2015 and 2016. Then, the harvested leaf and stem samples were killed at 105 °C for 30 min and then dried at 65 °C for at least 72 h to a constant mass in a drying oven.

#### Non-structural carbohydrates determination

The dry samples were ground and sifted by sieves with 0.25 mm mesh for NSCs measurement. In this study, NSCs was defined as soluble sugar plus starch (Hoch et al. 2003). The measurement methods of soluble sugar and starch referred to Li et al. (2011) with a little improvement. The stem samples and leaf samples of three tree species (each sample of 50 mg) were extracted three times with 25 ml of 75% ethanol at 80 °C for 30 min. The supernatants were combined in a 100 ml volumetric flask and diluted with 75% ethanol to volume. The solution was used to measure the amount of soluble sugar. The remaining pellets with 25 ml of 1% HCl were boiled for 2 h to decompose the starch. The anthrone colorimetry with glucose as the standard was adopted to determine the amount of soluble sugar and starch (Yemm and Willis 1954).

#### Environmental condition monitoring

We randomly chose two gaps from the eight experimental gaps, and set up data loggers (WatchDog 1650 Micro Station, Spectrum Technologies) to monitor environmental conditions (i.e., light availability, air temperature and relative air humidity, soil temperature, and soil moisture) at five within-gap positions in each gap during two growing seasons (2015 and 2016). Light availability (PAR: Photosynthetically Active Radiance), air temperature, and relative air humidity were automatically monitored at a height of 1.0 m above ground. Soil temperature and moisture were determined by External Temperature Sensors and SM 100 Soil Moisture Sensor, respectively, and the probes were buried at 5 cm below ground. All environmental

factors were recorded per 30 min. The mean values ( $\pm$  S.E.) of each environmental factor at five within-gap positions during two growing seasons are shown in Table 2.

#### Data analysis

A linear mixed model (LMM) was used to examine the effects of within-gap position and tree species on the concentrations of NSCs (total NSC, soluble sugar, and starch) in leaves and stems, the sprout growth characteristics (sprout height and basal diameter), sprout density and survival (i.e.,  $R_{e/b}$ ), and the ratio of leaf NSCs (total NSC, soluble sugar and starch) concentrations to stem NSCs (total NSC, soluble sugar, and starch) concentrations for 1-year-old sprouts and 2-year-old sprouts. In the model, within-gap position, tree species and the interaction of within-gap position and tree species were taken as fixed factors, and gap and stump diameter as random factors. The degrees of freedom for within-gap position, tree species and within-gap position  $\times$  tree species were 4, 2, and 8, respectively. Tukey's post hoc tests were used to further test differences among within-gap positions or among tree species.

Correlation analyses with the Pearson coefficient were conducted using all experimental stump data of each species at the end of these two growing seasons to test the correlations between stump diameter and concentrations of NSCs (total NSC, soluble sugar, and starch) in leaf and stem, and sprout density and survival ( $R_{e/b}$ ), and sprout growth (height and basal diameter) at the end of each growing season.

All of the statistical tests were performed using R (version 4.0.2) and significance was examined at the level  $P < 0.05$ . Log transformation was used when necessary to achieve normality and homogeneity of variance.

## Results

#### Sprout density, survival, and growth

Significantly positive correlations were found between stump diameter and sprout survival of 1-year-old *A. mono* ( $r = 0.54$ ;  $P = 0.04$ ), and between stump diameter

**Table 2** Mean ( $\pm$  S.E.) values of environmental factors at five within-gap positions during two growing seasons

Within-gap position	Photosynthetically active radiance (PAR) ( $\mu\text{M m}^{-2} \text{s}^{-1}$ )	Soil temperature (°C)	Soil moisture (%)	Air temperature (°C)	Air relative humidity (%)
North	152.75 $\pm$ 8.04	18.92 $\pm$ 0.41	15.79 $\pm$ 1.73	19.44 $\pm$ 0.52	71.71 $\pm$ 1.89
South	105.67 $\pm$ 8.30	17.40 $\pm$ 0.48	25.12 $\pm$ 3.74	19.00 $\pm$ 0.55	74.81 $\pm$ 1.90
East	129.46 $\pm$ 6.44	19.27 $\pm$ 0.46	15.28 $\pm$ 1.55	19.35 $\pm$ 0.53	71.81 $\pm$ 1.85
West	138.07 $\pm$ 6.59	18.04 $\pm$ 0.48	28.26 $\pm$ 2.35	19.49 $\pm$ 0.54	74.08 $\pm$ 1.94
Center	157.96 $\pm$ 7.22	19.42 $\pm$ 1.02	28.42 $\pm$ 2.56	19.43 $\pm$ 0.55	73.41 $\pm$ 1.88

and sprout density of 2-year-old *A. mono* ( $r = 0.79$ ;  $P < 0.001$ ) (Table 3). For *Q. mongolica*, stump diameter was positively correlated with the density and height of 1-year-old sprouts and the basal diameter of both two ages' sprouts ( $r > 0.50$ ;  $P < 0.05$ ) (Table 3). For *T. mandshurica*, only the 2-year-old sprout density was positively related to stump diameter ( $r = 0.75$ ;  $P = 0.00$ ) (Table 3).

There were no significant effects of within-gap position, tree species, and their interactions on sprout density, basal diameter, and survival of both 1-year-old sprouts and 2-year-old sprouts ( $P > 0.05$ ) (Table 4). Only tree species significantly affected the height of both two ages' sprouts ( $P < 0.05$ ) (Table 4). For 1-year-old sprouts, the sprout height of *A. mono* was significantly higher than that of *T. mandshurica* at the east of gap, and that of *Q. mongolica* at the west of gap ( $P < 0.05$ ) (Fig. 3b). For 2-year-old sprouts, the sprout height of *A. mono* was significantly higher than that of *Q. mongolica* at the north of gap, and that of *T. mandshurica* at the center of gap ( $P < 0.05$ ) (Fig. 3f).

#### Sprout NSCs concentrations

No significant relationship was found between stump diameter and NSCs concentrations of both two ages' sprouts for all three tree species ( $P > 0.05$ ). The within-gap position significantly affected the concentrations of leaf starch and NSC of 1-year-old sprouts and the concentrations of leaf soluble sugar and NSC of 2-year-old sprouts ( $P < 0.05$ ) (Table 5). There were significant effects of tree species on the concentrations of leaf NSCs (soluble sugar, starch and NSC) in both two ages' sprouts ( $P < 0.05$ ) (Table 5). The interaction of within-gap position and tree species significantly affected leaf starch concentration of 1-year-old sprouts ( $P = 0.01$ )

(Table 5). For 1-year-old sprouts, the maximum leaf soluble sugar concentration and total NSC concentration of *T. mandshurica* occurred at the south of forest gap, and significantly higher than those at the east, west, and center of gap ( $P < 0.05$ ) (Fig. 4a, c); and the leaf starch concentrations of *A. mono* at the north and center of gap were significantly lower than those at the south, east, and west of gap ( $P < 0.05$ ) (Fig. 4b). For 2-year-old sprouts, leaf soluble sugar and NSC concentrations of *Q. mongolica* at the north of gap were significantly lower than those at the other four within-gap positions, except for the leaf NSC concentration at the east of gap ( $P < 0.05$ ) (Fig. 4d, f); and the maximum of leaf NSCs concentrations of *T. mandshurica* occurred at the east of gap ( $P < 0.05$ ) (Fig. 4d–f).

Only tree species significantly affected stem NSCs concentration of both two ages' sprouts ( $P < 0.05$ ) (Table 5). The stem NSCs concentrations of 1-year-old *T. mandshurica* were significantly higher than those of 1-year-old *A. mono* and *Q. mongolica* ( $P < 0.05$ ) (Fig. 5a–c). The stem NSCs concentrations of 2-year-old *T. mandshurica* were significantly higher than those of 2-year-old *A. mono* ( $P < 0.05$ ) (Fig. 5d–f). Only the stem starch concentration of 2-year-old *Q. mongolica* was significantly affected by within-gap position, i.e., the stem starch concentration at the west of gap was significantly higher than that at the north of gap ( $P < 0.05$ ) (Fig. 5e).

Tree species significantly affected the ratio of leaf to stem NSC concentrations ( $\text{Ratio}_{\text{NSC}}$ ) and the ratio of leaf to stem starch concentrations ( $\text{Ratio}_{\text{S}}$ ) of both two ages' sprouts ( $P < 0.05$ ) (Table 5). There was a significant interaction effect of within-gap position and tree species on the  $\text{Ratio}_{\text{S}}$  of 1-year-old sprouts ( $P = 0.04$ ) (Table 5). Within-gap position significantly affected the ratio of leaf to stem soluble sugar concentrations of 2-year-old

**Table 3** Relationships between stump diameter and sprout density/growth/survival in both two growing seasons

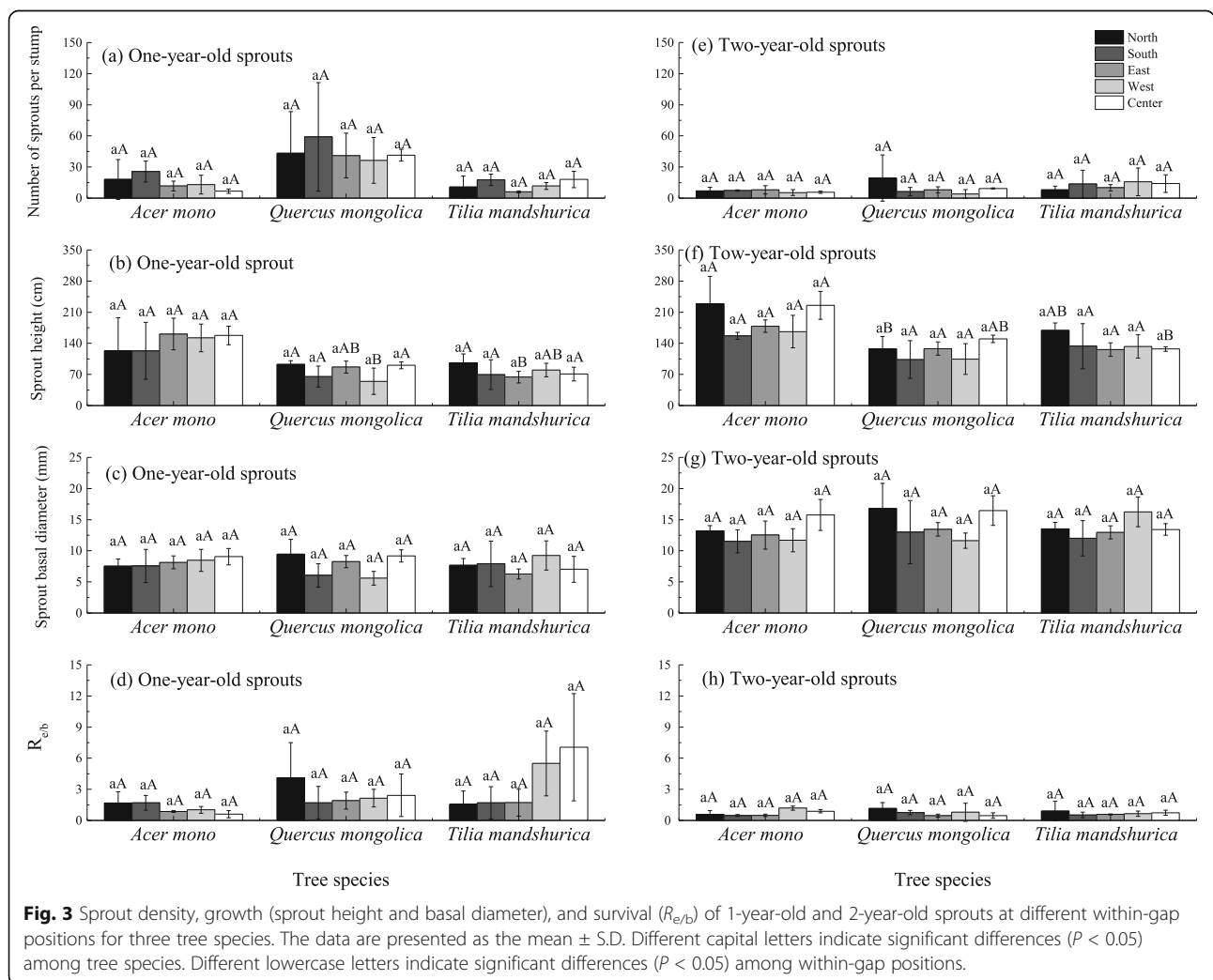
Tree species	Variables	One-year-old sprouts		Two-year-old sprouts	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>Acer mono</i>	SD	0.49	0.06	<b>0.79</b>	<b>&lt;0.001</b>
	SH	– 0.07	0.82	0.30	0.28
	SBD	– 0.01	0.97	0.12	0.68
	$R_{e/b}$	<b>0.54</b>	<b>0.04</b>	– 0.23	0.43
<i>Quercus mongolica</i>	SD	<b>0.54</b>	<b>0.04</b>	0.35	0.28
	SH	<b>0.58</b>	<b>0.03</b>	0.51	0.06
	SBD	<b>0.58</b>	<b>0.03</b>	<b>0.59</b>	<b>0.02</b>
	$R_{e/b}$	0.12	0.70	0.15	0.61
<i>Tilia mandshurica</i>	SD	– 0.10	0.73	<b>0.75</b>	<b>0.00</b>
	SH	– 0.16	0.58	0.26	0.40
	SBD	– 0.17	0.54	0.51	0.08
	$R_{e/b}$	0.05	0.87	– 0.20	0.50

Significant relationships ( $P < 0.05$ ) are bolded. SD sprout density, SH and SBD sprout height and basal diameter, respectively,  $R_{e/b}$  sprout survival

**Table 4** Effects of within-gap position and tree species on the sprout density, growth, and survival of 1-year-old and 2-year-old sprouts

Factors	df	Sprout density		Sprout height		Sprout basal diameter		Sprout survival	
		F	P	F	P	F	P	F	P
One-year-old									
WGP	4	1.18	0.44	1.20	0.46	1.22	0.45	0.39	0.81
TS	2	6.85	0.05	21.92	<b>0.02</b>	0.37	0.72	3.30	0.18
WGP × TS	8	0.32	0.92	0.66	0.72	1.39	0.43	1.93	0.32
Two-year-old									
WGP	4	0.33	0.85	3.72	0.16	2.40	0.25	0.93	0.55
TS	2	3.09	0.16	18.82	<b>0.02</b>	1.13	0.43	0.07	0.93
WGP × TS	8	1.31	0.42	0.88	0.61	1.38	0.46	1.42	0.43

Significant effects ( $P < 0.05$ ) are bolded. WGP within-gap position, TS tree species





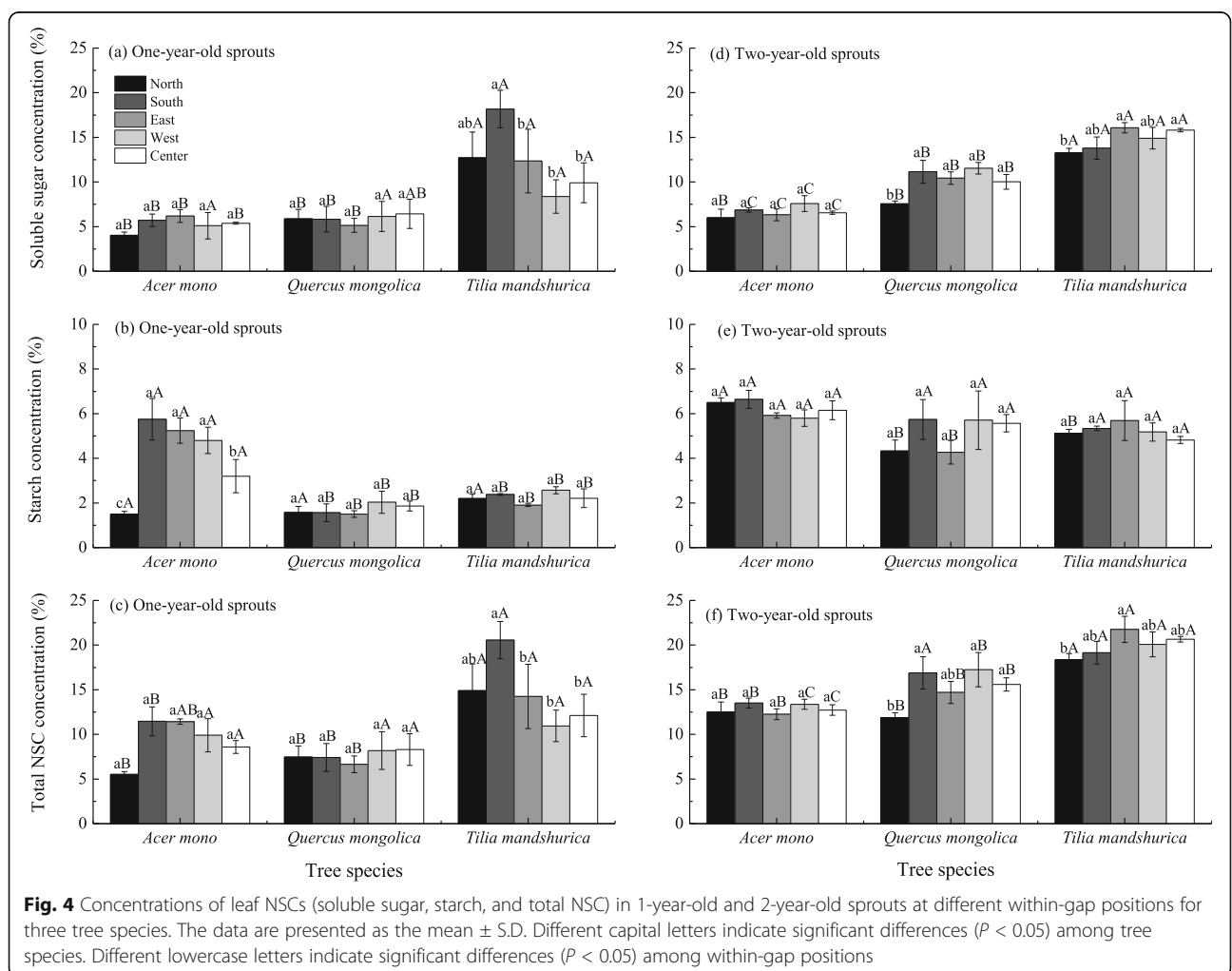
**Table 5** Effects of within-gap position and tree species on the concentrations of NSCs (soluble sugar, starch, and total NSC) and the ratios of leaf NSCs to stem NSCs in 1-year-old sprouts and 2-year-old sprouts

Factors	df	$C_{LSS}$		$C_{LS}$		$C_{LNSC}$		$C_{SSS}$		$C_{SS}$		$C_{SNSC}$		Ratio <sub>NSC</sub>		Ratio <sub>SS</sub>		Ratio <sub>S</sub>	
		F	P	F	P	F	P	F	P	F	P	F	P	r	P	r	P	r	P
One-year-old																			
WGP	4	5.89	0.06	17.72	<b>0.01</b>	6.67	<b>0.04</b>	1.54	0.34	1.25	0.42	1.31	0.40	4.54	0.09	2.59	0.19	6.08	0.05
TS	2	77.57	<b>0.00</b>	135.56	<b>0.00</b>	52.92	<b>0.00</b>	76.18	<b>0.00</b>	178.23	<b>0.00</b>	250.67	<b>0.00</b>	13.48	<b>0.02</b>	1.63	0.30	89.37	<b>0.00</b>
WGP × TS	8	4.80	0.07	19.55	<b>0.01</b>	5.33	0.06	1.12	0.49	1.77	0.30	2.42	0.21	4.89	0.07	3.96	0.10	7.05	<b>0.04</b>
Two-year-old																			
WGP	4	12.70	<b>0.02</b>	1.75	0.30	7.85	<b>0.04</b>	3.39	0.13	0.62	0.67	1.03	0.49	2.19	0.23	9.02	<b>0.03</b>	1.15	0.45
TS	2	407.05	<b>0.00</b>	16.63	<b>0.01</b>	171.67	<b>0.00</b>	50.03	<b>0.00</b>	158.48	<b>0.00</b>	183.60	<b>0.00</b>	42.80	<b>0.00</b>	0.36	0.72	169.91	<b>0.00</b>
WGP × TS	8	4.24	0.09	3.53	0.12	4.24	0.09	1.32	0.42	3.05	0.15	1.52	0.36	0.81	0.63	2.23	0.23	1.07	0.51

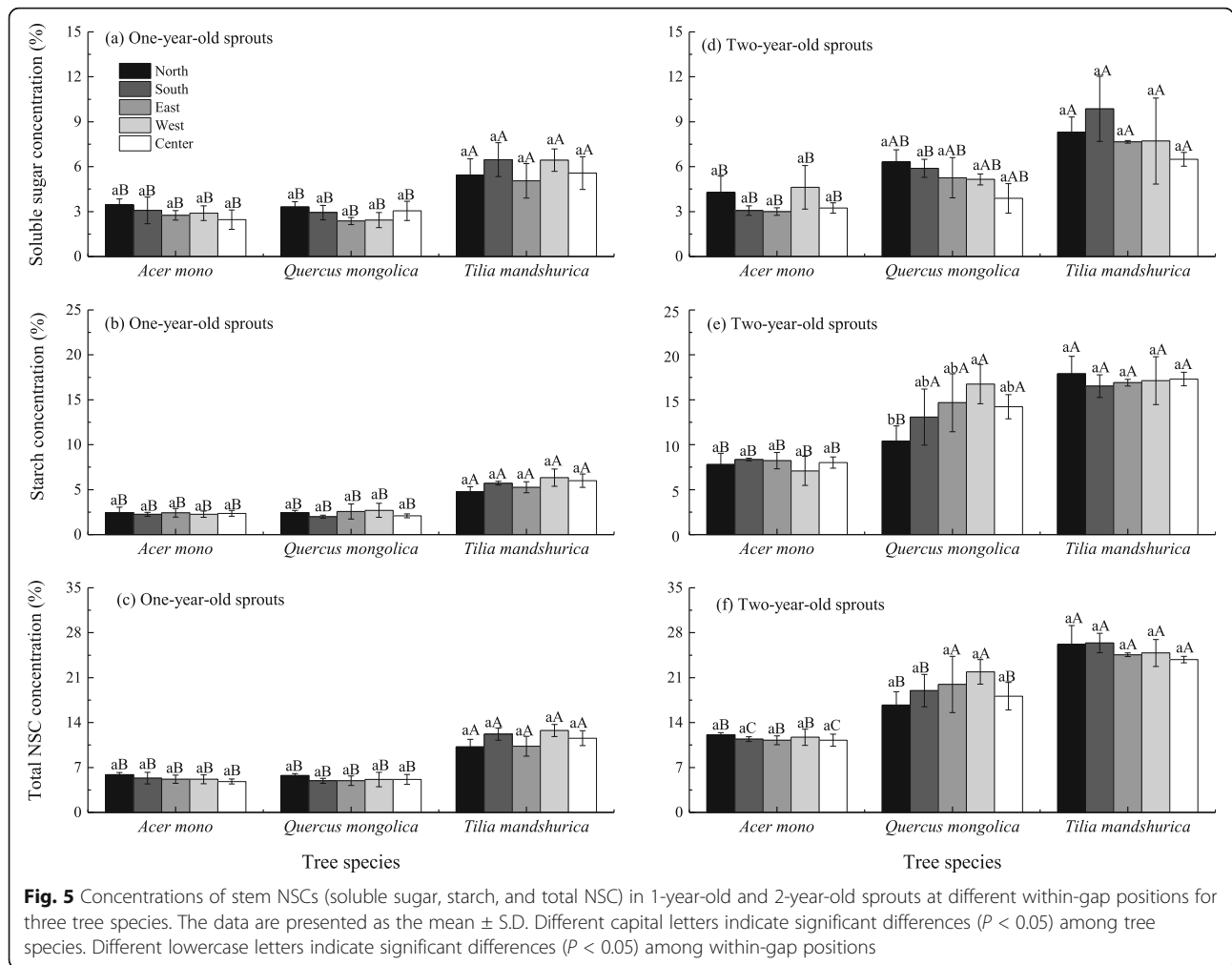
Significant effects ( $P < 0.05$ ) are bolded.  $C_{LSS}$  soluble sugar concentration in leaves,  $C_{LS}$  starch concentration in leaves,  $C_{LNSC}$  NSC concentration in leaves,  $C_{SSS}$  soluble sugar concentration in stems,  $C_{SS}$  starch concentration in stems,  $C_{SNSC}$  NSC concentration in stems, Ratio<sub>SS</sub>, Ratio<sub>S</sub>, and Ratio<sub>NSC</sub> the ratio of leaf to stem for soluble sugar, starch, and NSC concentrations, respectively, WGP within-gap position, TS tree species

sprouts ( $P = 0.03$ ) (Table 5). The Ratios<sub>S</sub> and Ratio<sub>NSC</sub> of *A. mono* at the north of gap were significantly lower than those at the south of gap ( $P < 0.05$ ) (Fig. 6b, c). The

Ratios<sub>S</sub> and Ratio<sub>NSC</sub> of *A. mono* were higher than those of *Q. mongolica* and *T. mandshurica* (Fig. 6e, f).



**Fig. 4** Concentrations of leaf NSCs (soluble sugar, starch, and total NSC) in 1-year-old and 2-year-old sprouts at different within-gap positions for three tree species. The data are presented as the mean ± S.D. Different capital letters indicate significant differences ( $P < 0.05$ ) among tree species. Different lowercase letters indicate significant differences ( $P < 0.05$ ) among within-gap positions



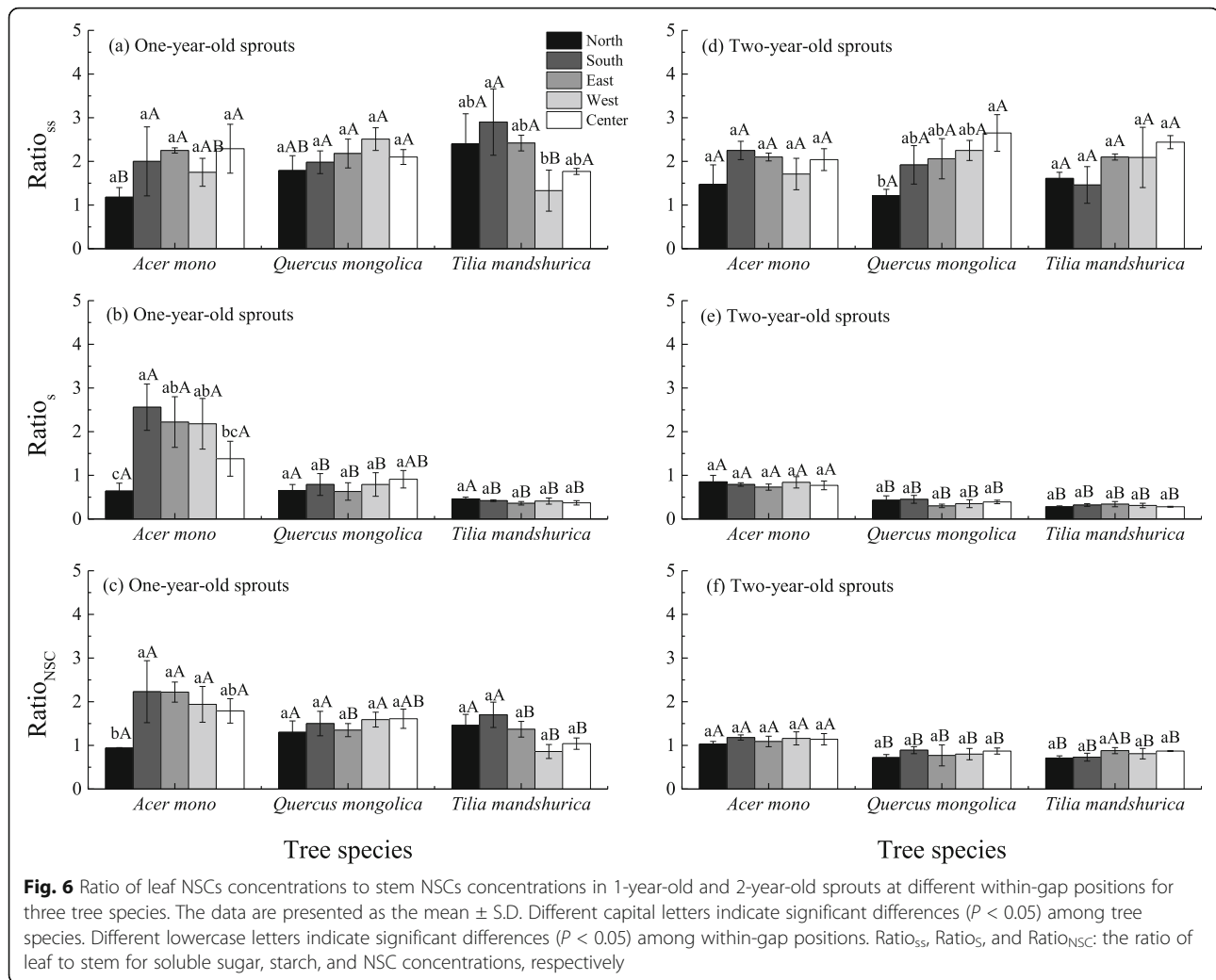
### Discussion

The temperate deciduous trees must accomplish all their physiological activities before the end of growing season (i.e., before dormancy), because carbon storage must be maintained during the dormant period to ensure carbon supply for the bud break and growth and refoliation in the spring of next year (Klein et al. 2016). In this research with the data of NSCs concentrations at the end of two growing seasons, we chose three temperate deciduous tree species with different shade tolerances to explore how the within-gap position (i.e., micro-environment) and stump size affect the survival, growth, and NSCs concentrations of stump sprouts at the early stage of gap formation.

The dormant buds or adventitious buds on the residues (e.g., stumps) of woody plants germinate to form sprouts, and the residues can provide nutrients and energy for sprout regeneration (Bond and Midgley 2001). Therefore, the stump size may affect sprout regeneration processes of woody plants. Stump diameter is an important predictor of sprout regeneration (Keyser and

Zarnoch 2014; Knapp et al. 2017). We examined the relationships between stump diameter and sprout density, growth, and survival of all three tree species, and found that all significant correlations were positive. The sprout survival and growth of two ages' *A. mono* and *Q. mongolica* were related to stump diameter, but stump diameter only significantly affected sprout density of 2-year-old *T. mandshurica*. These results indicated that the influence of stump diameter on sprout regeneration varies significantly among different tree species (Mwavu and Witkowski 2008; Knapp et al. 2017).

There is a trade-off between seedling growth and survival, and a fast growth rate is important for successful regeneration in gaps (Poorter and Kitajima 2007). However, our study found that the trade-off between sprout growth and survival was not significant at the early stage after gap formation. Moreover, sprout density, basal diameter, and survival presented insignificant difference among within-gap positions or tree species. These results are partly consistent with hypothesis 1, which is that the effect of stump diameter on sprout density,



**Fig. 6** Ratio of leaf NSCs concentrations to stem NSCs concentrations in 1-year-old and 2-year-old sprouts at different within-gap positions for three tree species. The data are presented as the mean  $\pm$  S.D. Different capital letters indicate significant differences ( $P < 0.05$ ) among tree species. Different lowercase letters indicate significant differences ( $P < 0.05$ ) among within-gap positions. Ratio<sub>SS</sub>, Ratio<sub>S</sub>, and Ratio<sub>NSC</sub>: the ratio of leaf to stem for soluble sugar, starch, and NSC concentrations, respectively

growth, or survival of all three tree species was significant, but the effect of within-gap position was slight.

The leaf NSCs concentrations of all three tree species were sensitive to the changes of micro-environment within a gap (i.e., within-gap positions) in both two growing seasons. According to the monitoring results of environmental condition within gap, the change of within-gap position mainly and directly affects the light condition (PAR value) and soil moisture (Table 2), and further can affect the process of photosynthesis in plant leaves (Ritter et al. 2005; He et al. 2012; Dietze et al. 2014). The NSCs accumulation depends on the photosynthesis (i.e., carbon source) (Hoch et al. 2003). Therefore, the leaf NSCs concentrations are more likely to be affected by the change of within-gap position, but there were interspecific differences in the response of leaf NSCs concentrations to the within-gap positions. Our result indicated that at the end of the first growing season after gap formation, the leaf NSCs concentration of *Q. mongolica* was independent of various within-gap

position. The concentrations of leaf soluble sugar and leaf total NSC of *T. mandshurica* were significantly higher at the south of gap (i.e., shadier and wetter micro-environment, Table 2), and the concentrations of leaf starch of *A. mono* were lower at the north of gap (i.e., lighter and drier micro-environment). To be better survival or growth, the seedling performances either conform to carbon gain hypothesis (maximize net carbon gain) or conform to stress hypothesis (resist biotic or abiotic stresses) (Valladares and Niinemets 2008). NSC storage is advantageous for seedlings survival and growth in stressful habitats (e.g., shaded habitats) (Iwasa and Kubo 1997; Myers and Kitajima 2007), and the carbon gain hypothesis also indicates that the shade-tolerant species should invest more in building leaf mass, leaf area, and leaf chlorophyll content to maximize the ability of light capture (Givnish 1988; McConnaughay and Coleman 1999; Zhang et al. 2013). Thus, compared with the shade intolerant *Q. mongolica*, the leaf carbohydrates storage performance of shade tolerant *T.*

*mandshurica* was consistent with carbon gain hypothesis. The lower leaf starch concentration of intermediate shade tolerant *A. mono* at the north of gap may be more consistent with stress hypothesis, since the lower soil moisture with the higher light condition at the north of gap (Table 2) might force the starch accumulation.

After an environmental adaption for two growing seasons, the effect of within-gap position on leaf NSCs concentrations of *A. mono* vanished, but the leaf NSCs concentrations of *Q. mongolica* and *T. mandshurica* exhibited significant differences among within-gap positions. The leaf NSCs concentrations of *Q. mongolica* showed a minimum value at the north of gap. However, the sprout height and basal diameter of *Q. mongolica* were higher at the north of gap. This may be because the habitat with higher light availability but lower soil moisture might lead to faster conversion of NSCs to structural carbon assimilation for promoting sprout growth (i.e., height and basal diameter increase) of shade intolerant *Q. mongolica*. The concentrations of leaf soluble sugar and leaf total NSC of 2-year-old *T. mandshurica* were maximum at the east of gap (i.e., shadier and drier micro-environment). This phenomenon might partly indicate that the shadier habitat was more beneficial for shade tolerant *T. mandshurica* to obtain leaf NSCs, and with the adapting to the environment, the soil moisture condition became the limiting factor. These results support hypothesis 2 that leaf NSCs concentrations are significantly affected by within-gap position and tree species.

In this study, the effect of within-gap position on the stem NSCs concentrations of all three tree species was not as significant as that on the leaf NSCs concentrations. This might be because the reserve carbohydrate levels in the boles and structural roots of trees would affect its ability to sprout and grow (Latt et al. 2001), and at the early stage of gap formation, the remaining stumps and roots retained a large amount of carbohydrates that could be used to partly compensate for the NSCs of stem growth. Only the influence of within-gap position on the stem NSCs concentrations of *Q. mongolica* began to appear at the end of the second growing season, and stem starch concentration showed the maximum value and minimum value at the west (i.e., moderate light and wetter micro-environment) and north (i.e., lighter and drier micro-environment) of gap, respectively. Kozłowski (1992) indicated that growth and development of cold hardiness were two of the essential roles of the storage carbohydrates for woody plants. NSCs reserved in stems supported plants to overcome the periods of stress and could promote the survival of plants (Poorter and Kitajima 2007). We tested the allocation of NSCs in leaves and stems of all three tree species. Within-gap position only significantly affected starch

and total NSC allocation of 1-year-old *A. mono* and soluble sugar allocation of 2-year-old *Q. mongolica*. The Ratio<sub>s</sub> and Ratio<sub>NSC</sub> of both two ages' sprouts varied among tree species. After two growing seasons' adaption, compared with *A. mono*, *Q. mongolica* and *T. mandshurica* allocated more starch and total NSC in stems than in leaves. The different responses of these three tree species might be because tree species with different shade tolerances would show varying carbon allocations to growth, defense, and storage in their natural habitats (Imaji and Seiwa 2010). Moreover, carbohydrates storage in the early autumn plays a crucial role in the carbon utilization of temperate deciduous tree species to manage the maintenance of respiration in the subsequent cold winter and bud break, leaf expansion, and growth in the next early spring (Wargo et al. 2002; Wong et al. 2003, 2009; Klein et al. 2016). Thus, from the perspective of stem NSC storage, our results partly indicated that *Q. mongolica* and *T. mandshurica* were easier to go through the winter and the vernal growth. These results were partly consistent with hypothesis 3, which is that stem NSCs concentrations were significantly affected by tree species, and the ratio of leaf to stem NSCs concentrations was significantly affected by tree species, but partly affected by within-gap position.

## Conclusions

At the early stage (2 years) after gap formation, stump diameter was positively correlated with sprout density, growth, and survival of all three tree species, but insignificantly related with sprout NSCs concentrations. Within-gap position significantly affected leaf NSCs concentrations of all three tree species, but most of sprout growth, survival, and stem NSCs concentrations were independent of the various within-gap positions. There were interspecific differences in the effects of within-gap position on sprout NSCs concentrations. At the end of the first growing season, leaf NSCs concentrations of shade intolerant *Q. mongolica* showed no significant difference among within-gap positions, but the leaf NSCs concentrations of intermediate shade tolerant *A. mono* and shade tolerant *T. mandshurica* were higher in the shadier micro-environment (e.g., south of gap). After 2 years environmental adaption, the influence of within-gap position on leaf NSCs concentrations changed. The effect of within-gap position on leaf NSCs concentrations of *A. mono* vanished. Habitat with higher light availability and lower soil moisture (i.e., north of gap) was not helpful for shade-intolerant *Q. mongolica* to accumulate leaf NSCs, and the shadier and drier habitat (i.e., east of gap) was conducive to increasing leaf NSCs concentrations of *T. mandshurica*. In conclusion, within-gap position significantly affected leaf NSCs concentrations, but had limited influence on sprout

regeneration (density, growth, and survival) of all three tree species. Besides stump diameter, the NSCs stored in stump and root systems and the interspecific differences in shade tolerance also contributed more to sprout regeneration at the early stage (2 years) of gap formation. A prolonged monitoring (> 10 years) is needed to further examine the long-term effects of stump diameter and within-gap position on sprout regeneration.

#### Abbreviations

NSCs: Non-structural carbohydrates; DBH: Diameter at breast height; WGP: Within-gap position; TS: Tree species; LMM: Linear mixed model

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#### Authors' contributions

QY and TZ conceived the ideas and designed the study. TZ conducted the field experiments, analyzed the data, and led the writing of the first draft of the manuscript. QY, JZ, and GW contributed to revising the manuscript. All authors read and approved the final manuscript.

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#### Availability of data and materials

Please contact the author for data requests.

#### Declarations

#### Ethics approval and consent to participate

Not applicable.

#### Consent for publication

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

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