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Synchronous and asynchronous root and shoot phenology in temperate woody seedlings

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24 **Abstract**

25 Understanding variation in root and shoot growth phenology among species is crucial to
26 understanding underlying mechanisms of temporal niche differentiation. However, little
27 is known about the relationship between root and shoot phenology, or how this
28 relationship varies among functional traits. We examined fine root and shoot phenology
29 of 42 seedlings representing a variety of woody species that inhabit the cool temperate
30 forests of northern Japan. Some aspects of phenology were common to the pool of
31 species examined: we found positive relationships between root and shoot phenology
32 for the end of growth, and for the duration of growth, but not for the start of growth.
33 Further, seedlings that started root growth relatively early also ended root growth
34 relatively late. Other aspects of phenology varied predictably with functional traits, i.e.
35 leaf habit and successional status: first, root growth in evergreen species started
36 significantly earlier and ended later than in deciduous species; second, early
37 successional species had the longest duration of shoot growth among all successional
38 types. Our results suggest that niche differentiation may be promoted by differences in
39 phenology between root and shoots, likely contributing to the co-existence of woody
40 seedlings in temperate forests.

41

42 **Keywords:** aboveground-belowground linkage, functional traits, leaf habit, species

43 coexistence, succession, temporal niche differentiation

44

Introduction

Growth phenology is closely linked to temporal variation in resource exploitation because the timing and duration of growth directly links to the quantity of a resource that plants can acquire (Pearman et al. 2008, Huang et al. 2019). Clarifying differences in growth phenology among species, growth forms and functional traits may contribute to understanding mechanisms of temporal niche differentiation (Fargione and Tilman 2005, Gonzalez and Loreau 2009).

Niche differentiation is known to be important in the early life stages of the trees (e.g. Peet 1985). At the same time, above-ground phenology has been well-documented in the early life stages of trees, and different phenological parameters are linked. For example, woody plants which start their shoot growth earlier often also end their growth earlier (Fu et al. 2014, Keenan and Richardson 2015, but see Panchen et al. 2014). This is thought to be because early bud burst and an early start of shoot growth results in a more rapid accumulation of the degree-days required for inducing dormancy, causing individuals to end their growth earlier (Fu et al. 2014, Keenan and Richardson 2015). Further, differences in growth phenology among individuals are related to functional traits (Lechowicz 2002, Panchen et al. 2014) and successional status. Leaf habit (e.g. evergreen versus deciduous leaves), height-related growth-form (tree or shrub), wood

anatomy (ring, diffuse or semi-ring porous) and species-specific successional status (pioneer or late successional) are useful for categorizing differences in aboveground phenology, such as the timing of shoot growth and leaf-out among woody individuals (Marks 1975, Maruyama 1979, Bicknell 1982, Boojh and Ramakrishnan 1982, Panchen et al. 2014).

In contrast, root phenology and its relation to shoot phenology have received less attention (Radville et al. 2016). Fine roots in seasonal climates often start to grow later than shoots (Hendrick and Pregitzer 1996, Joslin and Wolfe 1998, Steinaker and Wilson 2008, Iivonen et al. 2011, Abramoff and Finzi 2015), although there are notable exceptions to this pattern (Steinaker et al. 2010). Further, fine roots can continue to grow longer than shoots (Steinaker and Wilson 2008, Steinaker et al. 2010, Blume-Werry et al. 2016). Overall, the largest time-lags between the peaks of early shoot growth and later root growth appear to be between evergreen and deciduous trees (Abramoff and Finzi 2015). However the timing and number of pulses of root growth also shows a wide variation among species, as shown by the twelve temperate woody species (10 deciduous and 2 evergreen) studied by McCormack et al. (2014).

There are two main pathways linking root and shoot phenology. First, in seasonal ecosystems, similar temporal patterns of temperature and resource availability above-

and below ground (i.e., lower resource availability in winter and greater resource availability in summer) should drive convergence in root and shoot phenology. Second, root production is dependent on photosynthates assimilated above ground (Abramoff and Finzi 2015), which should also drive phenological convergence. Based on these facts, we expect shoot and root growth phenology to follow similar seasonal patterns. Specifically, we hypothesize that: 1) root and shoot phenology are correlated among woody plants within a temperate forest; and 2) leaf habit (deciduous vs. evergreen) is a strong predictor of variation in both shoot and root phenology, relative to other traits and successional status.

To test these hypotheses, we examined root and shoot phenology in 42 seedlings representing a phylogenetically wide range of species inhabiting the cool temperate forests of northern Japan. These species include both common and rare native species, as well as introduced species, representing a wide range of functional traits and successional status (Table 1). A key feature of our study is that we adopted a common garden approach in order to directly compare growth phenology across species.

Materials and Methods

99 *Phenology*

100 Phenology was measured in seedlings at the Forest Research Institute, Forest Research
101 Department, Hokkaido Research Organization, Japan (43°17'N, 141°51'E). The mean
102 annual temperature was 7.2 °C (January: -6.6 °C; August: 21.1 °C), and annual
103 precipitation was 1170 mm between 1981 – 2018 (Japan Meteorological Agency 2019).
104 The climate of the research site is Dfa (humid continental climate) in the Köppen
105 climate classification system.

106 One individual was measured for each of 42 species (Table S1, Supplementary
107 material). The rationale for this is that our focus was not on the growth phenology of
108 individual species, but rather on the relation of growth phenology to functional traits
109 across an evolutionarily large variety of trees. Most of the species are native to the
110 region, while a few (e.g. *Larix kaempferi*) were introduced for forestry and horticulture.
111 Seedlings (four to five years old) were planted in transparent pots (33 x 33 cm x 180 cm
112 deep) which were buried in soil in the nursery (Fig. 1). Pot depth was chosen to avoid
113 the suppression of root growth by shallow soil depth. One side of each pot was covered
114 with wooden blocks to allow periodic root measurements while otherwise eliminating
115 light and temperature fluctuations. Pots were filled with a mixture of brown upland
116 forest soil and volcanic sand.

Plants were measured every 1 – 2 weeks one year after planting. Measurements were conducted in 1981 (six species), 1983 (12 species), 1984 (12 species), and 1985 (12 species) (Table S1, Supplementary material), due to the time-consuming nature of the measurements. Differences in the year of measurement were taken into account in the statistical analysis (see below), and species of contrasting functional groups were planted in different years. For shoot growth, the length of the current-year's main shoot was measured. For root growth, the length of all roots that appeared on the transparent wall were measured. The start of growth was identified as the date (DOY) when the first root or shoot growth was detected. The end of growth was identified as the date when the final root or shoot growth was detected. These data were previously reported in the Ph.D thesis of Takao Sato (1994). We extracted data published as figures in the thesis using Web Plot Digitizer (Rohatgi 2012). The duration of growth was calculated as:

$$\text{Duration (days)} = \text{End of growth (DOY)} - \text{Start of growth (DOY)}$$

Functional traits

For each seedling, we determined the following functional traits: leaf habit (evergreen or deciduous, following Sato 2017); growth-form (tree or shrub); wood anatomy (ring-

porous, diffuse porous, or semi-ring porous wood, following Carlquist (2001) and using the Database of Wood Specimens run by the Forestry and Forest Product Research Institute in Japan <http://db.ffpri.affrc.go.jp/WoodDB/index-E.html>); successional status (early successional, early to middle successional, middle successional, middle to late successional and late successional, using Maruyama (1979), Koike (1988), and Bazzaz (2003)); and mycorrhizal type (ectomycorrhiza, arbuscular mycorrhiza, and ectomycorrhiza-arbuscular mycorrhiza). Wood anatomy is related to water uptake strategy (Lechowicz 2002, Takahashi et al. 2013). Height-related growth form (tree versus shrub) is related to rooting depth (Schenk and Jackson 2002). Successional status may influence root phenology because both light and soil resource availability vary across among successional stages (Marks 1975, Bicknell 1982, Vitousek et al. 1993). Mycorrhizal type influences the ability of plants to exploit belowground resources (Chen et al. 2016). Because we studied only one species that forms ericoid mycorrhiza, this species was excluded from the analysis of mycorrhizal type.

Analysis

We analyzed the relationship between shoot and root phenology with generalized linear mixed model (GLMM). The link function was set as log and the data set followed a

Gaussian distribution. The response variables were root phenological parameters and the explanatory variables were shoot phenological parameters. Furthermore, the relationships between the start and end of root growth, and between the start and end of shoot growth, were also analyzed.

We analyzed the relationship between phenology and functional traits with GLMM. Response variables were both shoot and root phenological parameters and the explanatory variable was set as each functional trait (see the tested traits, above). The data distribution of the response variables was assumed to follow a Gaussian distribution by setting the link function as log. The random factor was set as the year of the investigation to avoid the over-dispersion of the data across the years of investigation. The statistical significance was evaluated at $p < 0.05$. For the correlation between the two parameters in GLMM, conditional R^2 value (hereafter R^2C) was also calculated to show the variance explained (Nakagawa and Schielzeth 2013). We used the function “lme” in nlme package for GLMM analysis and in R. version 3.5.1. (R Core Team 2018).

Results

Relationships between root and shoot phenology

There was no significant relationship between the start of root and shoot growth (Fig. 2A). In contrast, there were significant positive relationships between the end of root and shoot growth (Fig 2B, $p=0.010$ and $R^2C=0.15$) and between the duration of root and shoot growth (Fig 2C, $p=0.018$ and $R^2C=0.15$). Seedlings with later end dates for root growth also had later end dates for shoot growth, resulting in a positive correlation between the duration of root and shoot growth.

Relationships between the start and end of growth

For roots, there was a negative correlation between the start and end of growth (Fig. 3A, $p<0.01$, $R^2C=0.31$). Seedlings with an early start of root growth tended to end root growth later than seedlings with a late start (Fig. 3A), suggesting that both an early start and late end of root growth contributed to a greater duration of root growth (note the distribution of circle sizes in Fig. 3A).

For shoots, there was no significant relationship between the start and end of growth (Fig.3B). Only the later end of shoot growth contributed to an increase of the duration of shoot growth (note circle size in Fig. 3B).

Phenology, functional traits and successional status

Evergreen seedlings started root growth significantly earlier and ended root growth significantly later than deciduous seedlings (Fig. 4A, B, Table 1, $p < 0.05$). Consequently, the duration of root growth of evergreen seedlings was about 30% longer than that of deciduous seedlings (Fig. 4C). Root phenology did not vary significantly with any other functional trait (Table 1).

For shoots, deciduous species started growth roughly 15 days earlier than evergreen species (Fig. 5A, Table 1, $p < 0.05$). The end and duration of shoot growth did not vary significantly between deciduous and evergreen species (Fig. 5B and C).

The end and the duration of shoot growth varied significantly with successional status (Table 1, $p < 0.05$). Early successional species had a significantly earlier start of shoot growth than late successional species (Fig. 6A). Further, seedlings of early successional species showed a later end of shoot growth as compared to mid and mid-late successional species (Fig. 6B). Overall, the seedlings of early successional species had the longest duration of shoot growth among all successional types (Fig. 6C). Life-form, mycorrhizal type and wood structure did not influence any aspect of the shoot growth variables (Table 1).

Discussion

Our examination of 42 woody species showed relationships between shoot and root phenology for the end and duration of growth. Further, we found that different functional traits predicted some aspects of root and shoot phenology. Together these findings imply that belowground phenological differentiation may contribute to co-existence in guilds of woody species with a given aboveground phenology.

Relationships between root and shoot phenology

There were significant positive correlations between roots and shoots for the duration and the end of growth, but not for the start of growth (Fig. 2). To our knowledge, this is the first study which demonstrates the presence and absence of correlations of growth phenology between shoot and fine root among woody seedlings within a forest type. The significant positive correlations might be due to the fact that fine root growth depends on the production and translocation of photosynthates (Abramoff and Finzi 2015, Radville et al. 2016). The later end of shoot growth might result in the later end of photosynthesis, resulting in later end dates for root growth. Another possibility is that similar seasonal patterns of resource availability above and below ground could contribute to the positive correlations, because both root and shoot phenology are influenced by environmental factors such as temperature and moisture (Pregitzer et al.

2000).

We note that, while significantly correlated, the proportion of variation in root phenology explained by shoot phenology was small both for the end and the duration of root growth (Fig. 2), which implies that factors beyond aboveground phenology (i.e., soil temperature and moisture) influence the growth phenology of fine roots. For example soil temperature and carbon allocation are both important regulators of root growth phenology in grapes (Comas et al. 2005).

Surprisingly, the start of shoot and root growth were not related (Fig. 2A). A reason for this could be that root growth may be fueled by the previous-year's carbon storage, thus translocation of non-structural carbohydrate from stems or coarse roots to fine root growth before the start of the shoot growth could make fine roots independent of the need to await the translocation of recently assimilated photosynthates. In fact, non-structural carbohydrates are known to influence the rate of root growth in spring (Nguyen et al. 1990, Eissenstat and Duncan 2012), although their importance for the timing of growth initiation is unclear. Our results provide further evidence that not only the duration of growth, but also the initiation of growth, may be influenced by photosynthate translocation (Abramoff and Finzi 2015).

In our study, root growth ended later than shoot growth, and the duration of root

growth was longer than shoot growth (Fig. 2B, C), which is consistent with previous studies of temperate trees and grasses, as well as arctic trees and shrubs (Steinaker and Wilson 2008, Steinaker et al. 2010, Blume-Werry et al. 2016). Underlying causes may include photosynthate translocation and high nutrient availability in autumn (Yokobe et al. 2018). Furthermore, the soil in our region does not freeze throughout the year owing to the thick snowpack in spite of air temperatures as low as -20 °C (Takagi et al. 2005), which may allow root growth in early winter, after shoots have stopped growing.

Relationships between the start and end of shoot and fine root growth

Previous studies have shown that species with an earlier start of shoot growth also end their growth earlier (Fu et al. 2014, Keenan and Richardson 2015), or that the start and end of aboveground growth were unrelated (Panchen et al. 2015). Surprisingly, when we tested these relationships for roots, we found that individuals with an early start of root growth ended their root growth later (Fig. 3). Data from McCormack et al. (2014) also suggest this pattern, but our study expands this finding to a larger array of species and functional traits. It is possible that an earlier start of root growth results in increased uptake of soil nutrients and water, which might stimulate shoot growth. This, in turn, may result in a positive feedback involving a longer period of shoot growth and

photosynthesis, allowing roots to grow for a longer period. Alternatively, species with short growth duration might have a more concentrated pattern of growth with a relatively high production of new tissue within a short period, which might be beneficial if resources are also temporally heterogeneous (McCormack et al. 2014).

For roots, both an earlier start and later end of growth contributed to longer growth duration, but for shoots, only growth at the end of the growing season contributed to a longer duration (Fig. 3). The reason that shoot duration was not influenced by the start of growth may be the well-known environmental constraints that exist early in the growing season in cool temperate forests. An earlier start of shoot growth is limited by the increasing risk of frost damage, while a later start is limited by seasonal light attenuation in temperate forests (Marks 1975, Bicknell 1982, Boojh and Ramakrishnan 1982). In cool temperate forests, suitable conditions for starting shoot growth (between spring frost and light attenuation) might last only briefly, which results in the simultaneous start of shoot growth (Lenz et al. 2016). As a result, the early start of shoot growth did not contribute to a longer duration of growth. In the case of roots, temperature generally fluctuates less in soil than in air, especially so in northern Japan where a thick snow cover prevents soil frost even at air temperature as low as -20 °C (Shibata et al. 2013). Therefore, fine roots are less threatened by frost than shoots,

which may result in divergence in the timing of root growth start between roots and shoots.

Phenology, functional traits and successional status

Among functional traits, only the evergreen-deciduous dichotomy contributed to differences in growth phenology of fine roots, probably because of the importance of the seasonality of carbon fixation and its allocation to root growth. Temperate evergreen species start photosynthesis earlier and end it later than deciduous species (Warren et al. 2011), and may start allocation to root growth earlier and end it later than do deciduous plants. Steinaker et al. (2010) reported the growth phenology of roots of four deciduous woody species and one evergreen woody species (*Picea*) from temperate forests. In their study, no clear difference between evergreen and deciduous plants was observed, which highlights the usefulness of including many species to categorize differences in root phenology among woody seedlings.

Our study found no evidence that differences in fine root growth phenology were related to wood anatomy, which relates to water uptake (Lechowicz 2002, Takahashi et al. 2013). Further, our results suggest that neither mycorrhizal type, which relates to the importance of fine root for its nutrient uptake (Chen et al. 2016), height-related growth-

form, which relates to rooting depth (Schenk and Jackson 2002), nor successional status were related to the difference in fine root phenology among woody species. These results suggest that the drivers of variation in root phenology may be less related to belowground resource availability than the activity of photosynthesizing apparatus.

Successional status explained variation in shoot phenology (Fig. 6) but not root phenology (Table 1), suggesting that different factors drive the evolution of growth phenology in fine roots and shoots. Successional status has been reported to be useful for categorizing interspecific differences in shoot phenology because light availability determines survival and growth (Marks 1975, Bicknell 1982, Boojh and Ramakrishnan 1982), which is consistent with our study. Here, seedlings of late successional species started shoot growth later than early successional species, possibly because they are typically shade-tolerant and can photosynthesize under the closed canopies that occur after leaf-out (Koike 1988). On the other hand, middle and middle-late successional species, which are sometimes categorized as gap species, have less shade tolerance than late successional species, which may be related to relatively greater carbon loss due to the higher rates of respiration (Loach 1967). Consequently, middle and middle-late successional species grew for a shorter period than did seedlings of early successional species (Fig. 6C).

Although soil resource availability, which varies across the successional stages (Walker and del Moral 2003), was expected to be related to root phenology, this relationship was not detected in our study. The lack of root phenological differences associated with successional status does not support a link between successional-ly determined nutrient availability and root phenology. Other aspects of root function may be important, e.g. early successional species have deeper roots than late successional species (Gale and Grigal 2008). However, our results indicate that co-existence of several species of the same successional status might be attributed partly to differences in belowground resource use between evergreen and deciduous species, which could promote forest diversity. However, we included too few early and middle successional evergreen species to explicitly examine variation in traits within a successional stage.

Our study examined only one seedling per species, and within-species differences could be quite large. One such source of intraspecific variation is the tremendous difference in size between seedlings and older trees. Seedlings and mature individuals of *Acer mono* differed greatly in shoot phenology (Seiwa 1999). Future studies could overcome this with replicates of each species, and including individual age or size as a factor. Further, the rooting volume in the pots used in our study differed from the rooting volume under the natural conditions experienced by seedlings in the field, but

we expect the range of responses revealed in the study to be representative of the range that would appear in the field.

In summary, our survey of 42 species found (1) positive relationships between shoot and root phenology for the end and the duration of growth but not for its initiation, (2) seedlings that started fine root growth relatively early ended their fine root growth relatively late, (3) root growth in evergreen species started significantly earlier and ended later than that in deciduous species and (4) early successional species had the longest duration of shoot growth among all successional types. Together, our results suggest that niche differentiation may be promoted by differences among species in the phenology of both above- and belowground tissues.

Contributions

MK designed the study, ST conducted the experiment, GBW, SDW and JHCC consulted on the analysis, and MK wrote the manuscript with help from SDW, GBW and JHCC.

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354

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452

Table

Table 1: The statistical significance of the influence of functional traits and successional status on interspecific differences of fine root and shoot growth phenology of seedlings tested by GLMM, “*” indicates statistical significance at $p < 0.05$, “n.s.” indicates no significant effect.

Parameter	Leaf habit	Growth form	Mycorrhizal type	Wood structure	Successional status
Start of shoot growth	*	n.s.	n.s.	n.s.	*
End of shoot growth	n.s.	n.s.	n.s.	n.s.	*
Duration of shoot growth	n.s.	n.s.	n.s.	n.s.	*
Start of root growth	*	n.s.	n.s.	n.s.	n.s.
End of root growth	*	n.s.	n.s.	n.s.	n.s.
Duration of root growth	*	n.s.	n.s.	n.s.	n.s.

Figure Captions

Figure 1: The rhizo-box used for root growth observations. The glass panel was covered with wooden blocks to avoid temperature fluctuation and light penetration into the soil profile.

Figure 2: Relationship of the A) start, B) end, and C) duration of growth between roots and shoots. The statistical significance for the relationship between the two parameters is shown as p value and the variation explained is shown as conditional R^2 value (R^2C). The solid line is the estimated relationship based on the GLMM analysis and the dashed line is the 1:1 line between the two parameters.

Figure 3: Relationship between the start and end of growth in fine roots (A) and shoots (B). Each circle shows the data of each individual. The size of each point shows the duration of growth. The statistical significance for the relationship between the two parameters is shown as p value and the variation explained is shown as conditional R^2 value (R^2C) respectively in each figure. The solid line is the estimated relationship based on the GLMM analysis.

Figure 4: The start (A), end (B) and duration (C) of fine root growth in deciduous and evergreen woody species. Different lower-case letters indicate significant differences between the groups ($p < 0.05$) analyzed with GLMM.

Figure 5: The start (A), end (B) and duration (C) of shoot growth in deciduous and evergreen woody species. Different lower-case letters indicate the statistically significant difference between the groups ($p < 0.05$) analyzed with GLMM.

Figure 6: The start (A), end (B) and duration (C) of shoot growth in woody species of contrasting successional stages. Early: early successional species; Early-Mid: species between early successional and middle successional species; Mid: middle successional species; Mid-Lat: species between middle successional and late successional species; and Late: late successional species. Different lower-case letters indicate statistically significant differences among the successional stages ($p < 0.05$, Tukey HSD).

493 **Figure 1**

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Supplementary material:

Table S1:

The list of the 42 woody species and their functional traits used in this study (derived from Carlquist (2001), Database of Wood Specimens of the Forestry and Forest Product Research Institute in Japan Maruyama (1979), Koike (1988), Bazzaz (2003), Lechowicz (2002), Takahashi et al. (2013)).

Species	Family	Investigation year	Growth form	Leaf habit	Mycorrhizal type	Wood structure	Successional status
<i>Abies sachalinensis</i>	Phaceae	1981	tree	ev	ECM	Tracheids	Late
<i>Acer ginnala</i> Maxim. var. <i>aiduense</i>	Sapindaceae	1983	trub	dc	AM	Diffuse	Mid-Late
<i>Acer mono</i>	Sapindaceae	1983	tree	dc	AM	Diffuse	Late
<i>Acer palmatum</i> var. <i>matsumurae</i>	Sapindaceae	1983	tree	dc	AM	Diffuse	Late
<i>Acer ukurunduense</i>	Sapindaceae	1983	trub	dc	AM	Diffuse	Early-Mid
<i>Aesculus turbinata</i>	Sapindaceae	1983	tree	dc	AM	Diffuse	Early-Mid
<i>Alnus hirsuta</i>	Betulaceae	1984	tree	dc	AM-ECM	Diffuse	Early
<i>Alnus maximowiczii</i>	Betulaceae	1984	tree	dc	AM-ECM	Diffuse	Early
<i>Betula platyphylla</i>	Betulaceae	1983	tree	dc	ECM	Diffuse	Early
<i>Carpinus cordata</i>	Betulaceae	1984	tree	dc	ECM	Diffuse	Late
<i>Castanea crenata</i>	Fagaceae	1984	tree	dc	ECM	Ring	Early-Mid
<i>Cerasus sargentii</i>	Rosaceae	1983	tree	dc	AM-ECM	Diffuse	Mid-Late
<i>Cercidiphyllum japonicum</i>	Cercidiphyllaceae	1981	tree	dc	AM	Diffuse	Mid
<i>Cornus controversa</i>	Cornaceae	1985	tree	dc	AM	Diffuse	Mid
<i>Corylus sieboldiana</i>	Betulaceae	1984	shrub	dc	ECM	Diffuse	Early-Mid
<i>Elaeagnus umbellata</i>	Elaeagnaceae	1985	shrub	dc	AM	Ring	
<i>Euonymus alatus</i>	Celastraceae	1985	shrub	dc	AM-ECM	Diffuse	Mid
<i>Fraxinus mandshurica</i> var. <i>japonica</i>	Oleaceae	1984	tree	dc	AM	Ring	Early-Mid
<i>Hydrangea paniculata</i>	Hydrangeaceae	1985	shrub	dc	AM	Diffuse	Early
<i>Ilex crenata</i> var. <i>pakidosa</i>	Aquifoliaceae	1984	shrub	ev	ECM	Diffuse	Early
<i>Juglans mandshurica</i> var. <i>sachalinensis</i>	Juglandaceae	1984	tree	dc	AM	Semi-ring	Mid
<i>Kalopanax septemlobus</i>	Araliaceae	1983	tree	dc	AM	Ring	Mid
<i>Larix kaempferi</i>	Phaceae	1981	tree	dc	ECM	Tracheids	Early
<i>Loniceria caerulea</i> var. <i>emphyllcalyx</i>	Caprifoliaceae	1985	shrub	dc	AM	Diffuse	
<i>Maackia amurensis</i> var. <i>buergeri</i>	Fabaceae	1985	tree	dc	AM-ECM	Ring	Mid
<i>Magnolia praecoxissima</i> var. <i>borealis</i>	Magnoliaceae	1981	tree	dc	AM	Diffuse	Early-Mid
<i>Malus toringo</i>	Rosaceae	1985	trub	dc	AM-ECM	Diffuse	Early-Mid
<i>Morus australis</i>	Moraceae	1984	trub	dc	AM-ECM	Ring	Early-Mid
<i>Padus grayana</i>	Rosaceae	1983	tree	dc	AM-ECM	Diffuse	Mid-Late
<i>Phellodendron amurense</i>	Rutaceae	1984	tree	dc	AM	Ring	Early-Mid
<i>Picea glehnii</i>	Phaceae	1981	tree	ev	ECM	Tracheids	Late
<i>Populus suaveolens</i>	Salicaceae	1985	tree	dc	AM-ECM	Diffuse	Early
<i>Quercus crispula</i>	Fagaceae	1983	tree	dc	ECM	Ring	Mid-Late
<i>Rhamnus japonica</i> var. <i>deciensis</i>	Rhamnaceae	1985	shrub	dc	AM	Diffuse	
<i>Rhododendron brachycarpum</i>	Ericaceae	1984	shrub	ev	ERM	Semi-ring	Mid
<i>Rosa rugosa</i>	Rosaceae	1985	shrub	dc	AM-ECM	Ring	Early
<i>Sorbus commixta</i>	Rosaceae	1983	tree	dc	AM-ECM	Diffuse	Mid
<i>Styrax japonica</i>	Styraceae	1985	trub	dc	AM	Diffuse	
<i>Syringa reticulata</i>	Oleaceae	1985	tree	dc	AM	Diffuse	Mid
<i>Taxus cuspidata</i>	Taxaceae	1981	tree	ev	AM	Tracheids	Late
<i>Tilia japonica</i>	Malvaceae	1984	tree	dc	ECM	Diffuse	Mid-Late
<i>Ulmus davidiana</i> var. <i>japonica</i>	Ulmaceae	1983	tree	dc	AM	Ring	Early-Mid