Changes in stand structure and biomass increment in a warm temperate forest at a long-term ecological research site in Korea over 17 years

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**ABSTRACT**

Changes in stand biomass, stem density, mortality and recruitment were monitored from 2000 to 2016 at 5- or 6-year intervals of Mt. Geumsan (GMS). The GMS had 34 woody plant species and 2698 living stems (DBH ≥ 2 cm) ha⁻¹ in 2016, with an increase in biomass from 233.80 ton ha⁻¹ in 2000 to 282.15 ton ha⁻¹ in 2016. The dominant species in the canopy layer was *Quercus serrata*, while *Chamaecyparis obtusa* was the dominant species in the sub-tree layer. During the 17 years, the biomass of *Q. serrata* increased from 156.33 to 198.40 ton ha⁻¹, while the stem density of *Q. serrata* declined from 395 to 268 stems ha⁻¹. In addition, the biomass of *C. obtusa* increased from 12.70 to 24.09 ton ha⁻¹, and also the stem density of *C. obtusa* increased from 722 to 898 stems ha⁻¹. The forest structure of GMS is expected to maintain dominance of *Q. serrata*, and *C. obtusa* is increasing. Therefore, GMS was a natural broad-leaved forest composed of *Q. serrata*, but natural broad-leaved species at the site are declining due to the regeneration and growth of *C. obtusa*, which is relatively shade-tolerant compared to other species.

**Introduction**

Balance in the global carbon is a major current issue because carbon concentration in the atmosphere affects climate both at a global and local scale (Zhao et al. 2019). Forest ecosystems are one of the major carbon sinks, with 45% of the carbon found in the terrestrial biosphere being stored and exchanged (Bonan 2008; Zhao et al. 2019). Forest ecosystems are one of the major carbon sinks, with 45% of the carbon found in the terrestrial biosphere being stored and exchanged (Bonan 2008; Zhao et al. 2019). Forest ecosystems are one of the major carbon sinks, with 45% of the carbon found in the terrestrial biosphere being stored and exchanged (Bonan 2008; Zhao et al. 2019). Forest ecosystems are one of the major carbon sinks, with 45% of the carbon found in the terrestrial biosphere being stored and exchanged (Bonan 2008; Zhao et al. 2019). Forest ecosystems are one of the major carbon sinks, with 45% of the carbon found in the terrestrial biosphere being stored and exchanged (Bonan 2008; Zhao et al. 2019).

Trees in a forest ecosystem assimilate or release carbon from and to the atmosphere, and these processes are regulated by the growth of trees (Thom et al. 2017). Therefore, understanding forest stand dynamics of forest ecosystems is fundamental to understand terrestrial carbon cycling and can be observed through changes in recruitment, growth and mortality of stems and growth of stems in forest stands (Bordin and Müller 2019). In addition, knowledge of forest stand dynamics offers insights into the structure of the current forest stand and future forest ecosystem (Swetnam et al. 1999).

Forest succession is driven mainly by interspecific differences in life-history traits such as shade tolerance, as slow-growing shade-tolerant species replace relatively shade-intolerant species (Kobe et al. 1995). Shade tolerance is a key component of tree fitness and the foundation of current theories of forest succession in forests (Valladares and Niinemets 2008). Shade tolerance is considered an important factor in forest succession because the difference between light competition and shade tolerance is an important determinant of forest structure and dynamics (Canham et al. 1994; Gravel et al. 2008). The mortality of trees depends on the rate and stage of stand development and frequency of disturbance (Harcombe et al. 1990). Trees die for a variety of reasons such as competition, suppression, old age, disease, insect pests, and other environmental stressors (Lugo and Scatena 1996). The recruitment of shade-tolerant species can occur in old forests (Franklin et al. 2002), and young trees can grow slowly, leading to stems that last for decades (Henttonen et al. 2019).

South Korea has a large forested area covering approximately 63% in 2020 of the total land area (100,000 km²) (National Institute of Forest Science 2011). The Korea Long-Term Ecological Research (KLTER) network was established in 2000 in the Mt. Geumssan (GMS) area of, Korea by the National Institute of Forest Science (NIFoS). GMS is registered as an official site in the International Long-Term Ecological Research-Dynamic Ecological Information Management System (ILTER-DEIMS, https://deims.org/). The dominant species at the GMS site are *Quercus serrata* Thunb. Ex Murray, *Chamaecyparis obtusa* (Siebold & Zucc.) Endl, *Carpinus tschonoskii* Maxim., and *Carpinus laxiflora* (Siebold & Zucc.) Blume (Yun and Chun 2018). These tree species are widely distributed throughout East Asia (Kira 1991), and *Q. serrata*, *C. tschonoskii*, and *C. laxiflora* are common throughout South Korea. However, *C. obtusa* is limited to the southern part of South Korea. *C. obtusa* has been planted in the southern region in South Korea...
Korea since the 1960s, becoming one of the most important plantation species in South Korea, *C. obtusa* accounted for about 34.05% of the total planted area (14,542 ha) in 2019 (Korean Forest Service 2020).

The aim of this study was to investigate how the stand structure, species composition, and biomass in the warm temperate forest of GMS have changed over 17 years. For this purpose, the number of stems, basal area (BA), biomass, mortality, recruitment rate, and relative growth rate of DBH and height were monitored in a 1-ha permanent plot at GMS over 17 years.

**Methods**

**Study site**

The present study was conducted at the GMS (34°45′N, 127°59′E) LTER site on the southern coast of the Hallyeohaesang National Park in Gyeongsangnam-do, Korea (Figure 1). A 1-ha study plot (100 m × 100 m) was established in 2000 and was divided into 100 subplots of 100 m² by compass surveying. The area is located in a warm-temperate forest zone. The long-term (1981–2010) annual mean temperature and precipitation at this site were 14.1 °C and 1839.4 mm, respectively (Korea Meteorological Administration 2015). GMS is situated at a 360–430 m hillside elevation with slopes ranging from 12–28°.

**Data collection**

All individual woody stems ≥2 cm diameter at breast height (DBH) were identified to species, tagged, and measured using a diameter tape, and tree heights were measured using a Vertex hypsometer (Vertex IV, Haglöf, Sweden). The plot was re-censused in 2006, 2011, and 2016. The precise identification and scientific names of trees were confirmed by the National Knowledge and Information System for Biological Species of Korea (www.nature.go.kr) and a checklist of vascular plants in Korea (Korea National Arboretum, 2007).

**Plant mortality and recruitment**

The annual mortality rates (%year⁻¹) and recruitment rates (%year⁻¹) were calculated by the following:

\[
\text{Mortality rates} = \ln\left(\frac{N_0}{N_s}\right) \times 100/t,
\]

\[
\text{Recruitment rates} = \ln\left(\frac{N_f}{N_s}\right) \times 100/t
\]

where \(N_0\) is the initial number of stems initial census, \(N_s\) is the number of surviving stems among the initial censused trees, and \(N_f\) is the total number of stems during the census period (t years) (Condit et al. 1995; Sheil and May 1996; Condit et al. 1999).
Relative growth rate of DBH and height

The relative growth rate of DBH (RGRD) and height (RGRH) were calculated as follows:

\[
\text{RGRD} = \left( \frac{D_2 - \ln D_1}{t_2 - t_1} \right),
\]

\[
\text{RGRH} = \left( \frac{H_2 - \ln H_1}{t_2 - t_1} \right)
\]

where \(D_2, H_2\) and \(D_1, H_1\) are the initial and final measurements for DBH and height, respectively, and \(t_2\) and \(t_1\) represent the time interval (Evans 1972).

Biomass estimate

Biomass was calculated for each stem using species-specific allometric equations. Five tree species that had a high proportion of stand basal area were selected as dominant species. Thirty-four tree species were recorded in all field plots and classified as five types for more accurate biomass estimate: (1) Quercus serrata, (2) Carpinus tschonoskii, (3) C. laxiflora, and (5) other tree species. The DBH and height of Q. serrata, C. obtusa, and C. laxiflora were used to estimate their biomass using different biomass allometric equations (Table 1) (National Institute of Forest Science 2010). The biomass equation of C. tschonoskii used the biomass equation of C. laxiflora, which is in the same genus, Carpinus. And the biomass of other tree species was estimated using the biomass equation reported by Lim et al. (2003). Total biomass production in the plots was obtained by summing the biomass of all the standing trees.

Results

The total numbers of stems (DBH ≥ 2 cm) at the 1 ha permanent plot (trees ha\(^{-1}\)) in 2000, 2006, 2011, and 2016 were 3933, 3563, 3055, and 2698, respectively. A total number of species was 34 species and it did not change during the survey period. The species with a high proportion of stand BA were Q. serrata, C. tschonoskii, C. laxiflora, and C. obtusa. Aside from these, Pinus densiflora Siebold & Zucc, Acer pseudosieboldianum (Pax) Kom, Styrax japonicus Siebold & Zucc, Stewartia pseudocamellia Maxim. and others were observed.

The number of Q. serrata stems continued to increase from 395 trees ha\(^{-1}\) in 2000 to 268 trees ha\(^{-1}\) in 2016, but C. obtusa stems continued to increase from 722 trees ha\(^{-1}\) in 2000 to 898 trees ha\(^{-1}\) in 2016 (Figure 2). The number of Q. serrata was only 268 trees ha\(^{-1}\) (9.93%), and the sum of BA was 18.73 m\(^2\)ha\(^{-1}\) in 2016 (55.48%) (Table 2). In contrast, the number of C. obtusa was 898 trees ha\(^{-1}\) (33.28%), while the sum of BA was 4.38 m\(^2\)ha\(^{-1}\) in 2016 (12.98%). The difference in the number of Q. serrata and C. obtusa between 2000 and 2016 is due to the different numbers of dead trees and recruited trees. The number of dead trees of Q. serrata was 127 trees ha\(^{-1}\) over 17 years since 2000, while there was no tree recruitment. Meanwhile, the number of dead trees of C. obtusa was 163 trees ha\(^{-1}\) during the same period, and the number of recruited trees was 339 trees ha\(^{-1}\).

The average DBH of Q. serrata, C. obtusa, C. tschonoskii, C. laxiflora, and other tree species continuously increased over the 17 years in 2016. The average DBH of Q. serrata was the largest, with 28.19 ± 0.60 cm, and C. obtusa was the smallest at 5.90 ± 0.17 cm in 2016. Likewise, the average height of Q. serrata, C. obtusa, C. tschonoskii, C. laxiflora, and other tree species also continuously increased over the 17 years. The average height of Q. serrata was the largest, 18.09 ± 0.17 m, and C. obtusa was the smallest, at 5.24 ± 0.11 m.

Meanwhile, the number of stems and BA of other tree species (P. densiflora, A. pseudosieboldianum, S. japonicus, S. pseudocamellia, etc.) continually decreased over 17 years. Among them, A. pseudosieboldianum, which decreased from 395 trees ha\(^{-1}\) in 2000 to 327 trees ha\(^{-1}\) in 2016, accounted for the largest number of stems of other tree species. The number of stems of S. japonicus continuously decreased from 346 trees ha\(^{-1}\) in 2000 to 149 trees ha\(^{-1}\) in 2016, and the number of stems of S. pseudocamellia continuously decreased from 262 trees ha\(^{-1}\) in 2000 to 115 trees ha\(^{-1}\) in 2016.

The number of stems and sum of BA of P. densiflora among other tree species has also been continuously decreasing over 17 years, from 40 trees ha\(^{-1}\) in 2000 to 16 trees ha\(^{-1}\) in 2016. The sum of BA of P. densiflora decreased from 1.64 m\(^2\)ha\(^{-1}\) in 2000 to 1.02 ± m\(^2\)ha\(^{-1}\) in 2016.

The mean relative growth rate of DBH and height of dominant tree species varied over the survey period (Table 3). However, the mean annual relative growth of DBH and height in each dominant tree species showed a similar pattern during the three survey periods. The mean annual relative growth rate (mm year\(^{-1}\)) of DBH of Q. serrata in each survey interval was 0.09 ± 0.005, 0.10 ± 0.004, and 0.08 ± 0.005, respectively. The mean relative growth rate of height (cm year\(^{-1}\)) of Q. serrata in each survey interval was 1.36 ± 0.118, 0.66 ± 0.107, and 0.76 ± 0.071, respectively. Similarly, the mean annual relative growth rate of DBH (mm year\(^{-1}\)) of C. obtusa in each survey interval was 0.26 ± 0.013, 0.27 ± 0.007, and 0.25 ± 0.008, respectively, while the

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**Table 1. Allometric equations used to estimate biomass of Quercus serrata, Chamaecyparis obtusa, Carpinus tschonoskii, C. laxiflora, and other tree species.**

| Tree species          | Component | Allometric equation |
|-----------------------|-----------|---------------------|
| Quercus serrata       | Stem      | \( Y = 0.0460D^{0.989}H^{0.799} \) |
|                       | Branch    | \( Y = 0.0190D^{3.34}H^{0.923} \) |
|                       | Leaf      | \( Y = 0.0089D^{2.98}H^{0.785} \) |
|                       | Root      | \( Y = 0.276D^{3.35}H^{0.355} \) |
|                       | Stem      | \( Y = 0.0260D^{2.70}H^{0.199} \) |
|                       | Branch    | \( Y = 0.050D^{5.74}H^{0.639} \) |
|                       | Needle    | \( Y = 0.369D^{2.03}H^{0.127} \) |
|                       | Root      | \( Y = 0.706D^{2.03}H^{0.637} \) |
|                       | Stem      | \( Y = 0.107D^{3.97}H^{1.884} \) |
|                       | Leaf      | \( Y = 0.003D^{3.87}I^{1.491} \) |
|                       | Root      | \( Y = 0.045D^{3.37}I^{0.501} \) |
| Carpinus tschonoskii  | Stem      | \( Y = 0.065D^{2.909} \) |
|                       | Branch    | \( Y = 0.107D^{3.70}H^{1.884} \) |
|                       | Leaf      | \( Y = 0.003D^{3.37}I^{0.501} \) |
|                       | Root      | \( Y = 0.045D^{2.909} \) |
|                       | Stem      | \( Y = 0.065D^{2.58}H^{1.884} \) |
|                       | Leaf      | \( Y = 0.003D^{3.37}I^{0.501} \) |
|                       | Root      | \( Y = 0.045D^{2.909} \) |
| Carpinus laxiflora    | Stem      | \( Y = 0.065D^{3.87}I^{1.491} \) |
|                       | Branch    | \( Y = 0.107D^{3.70}H^{1.884} \) |
|                       | Leaf      | \( Y = 0.003D^{3.37}I^{0.501} \) |
|                       | Root      | \( Y = 0.045D^{3.37}I^{0.501} \) |
| Other tree species    | Deciduous species | \( Y = 0.167D^{3.395} \) |
|                       | Conifer species | \( Y = 0.086D^{3.395} \) |

\(^*Y\) is the biomass of the tree component (kg). \(D\) is the diameter at breast height (cm), and \(H\) is the tree height (m) (1) National Institute of Forest Science 2010; (2) Lim et al. 2003.
The mean relative growth rate of height (cm year\(^{-1}\)) of *C. obtusa* in each survey interval was 3.00 ± 0.097, 2.51 ± 0.120, and 1.10 ± 0.126, respectively.

The DBH size distribution of the dominant tree species differed with species (Figure 3). At the species level, the DBH size distribution of the dominant tree, *Q. serrata* showed a right-skewed distribution; the peak was in the 20–25 cm class and a few recruitment stems (2–5 cm) were observed. In addition, *C. tschonoskii* and *C. laxiflora* showed a right-skewed distribution; the peak was in the

![Figure 2](image-url). Sequential changes in the number of stems (trees ha\(^{-1}\)), and biomass (ton ha\(^{-1}\)) in GMS from 2000 to 2016.

### Table 2. Sequential changes in the sum of basal area (m\(^2\)ha\(^{-1}\)), average of DBH (cm), and average of height (m) of dominant tree species from 2000 to 2016.

| Species               | Sum of basal area (m\(^2\)ha\(^{-1}\)) | Average of DBH (cm) | Average of height (m) |
|-----------------------|-------------------------------------|---------------------|----------------------|
|                       | 2000  | 2006  | 2011  | 2016  | 2000  | 2006  | 2011  | 2016  | 2000  | 2006  | 2011  | 2016  |
| *Quercus serrata*     | 16.18 | 17.33 | 17.73 | 18.73 | 20.76 | 23.38 | 26.46 | 28.19 | 14.25 | 15.97 | 17.22 | 18.09 |
|                       | (±0.48) | (±0.52) | (±0.57) | (±0.60) | (±0.20) | (±0.19) | (±0.17) | (±0.17) |
| *Chamaecyparis obtusa* | 2.44  | 3.05  | 3.71  | 4.38  | 4.74  | 5.05  | 5.31  | 5.90  | 4.32  | 4.72  | 5.05  | 5.24  |
|                       | (±0.16) | (±0.16) | (±0.16) | (±0.17) | (±0.11) | (±0.11) | (±0.11) | (±0.11) |
| *Carpinus tschonoskii* | 2.32  | 2.42  | 2.43  | 2.55  | 10.59 | 12.38 | 13.94 | 15.07 | 9.22  | 10.98 | 12.00 | 12.54 |
|                       | (±0.47) | (±0.55) | (±0.64) | (±0.69) | (±0.27) | (±0.31) | (±0.33) | (±0.38) |
| *Carpinus laxiflora*  | 1.33  | 1.49  | 1.49  | 1.50  | 11.19 | 12.43 | 14.26 | 15.63 | 10.26 | 11.21 | 12.33 | 13.28 |
|                       | (±0.70) |(±0.77) |(±0.90) |(±0.98) |(±0.42) |(±0.45) |(±0.51) |(±0.52) |
| Other tree species     | 8.77  | 8.54  | 7.55  | 6.60  | 5.26  | 5.67  | 6.16  | 6.43  | 5.61  | 6.38  | 6.85  | 7.11  |
|                       | (±0.08) |(±0.09) |(±0.11) |(±0.12) |(±0.06) |(±0.06) |(±0.08) |(±0.10) |

Numbers in parentheses indicate standard error of the mean.

### Table 3. The mean relative growth rate of DBH and height of dominant tree species.

| Species               | DBH (mm year\(^{-1}\)) | Height (cm year\(^{-1}\)) |
|-----------------------|------------------------|---------------------------|
|                       | 2000–2006 | 2006–2011 | 2011–2016 | 2000–2006 | 2006–2011 | 2011–2016 |
| *Quercus serrata*     | 0.09 (±0.005) | 0.10 (±0.004) | 0.08 (±0.005) | 1.36 (±0.118) | 0.66 (±0.107) | 0.76 (±0.071) |
| *Chamaecyparis obtusa*| 0.26 (±0.013) | 0.27 (±0.007) | 0.25 (±0.008) | 3.00 (±0.097) | 2.51 (±0.120) | 1.10 (±0.126) |
| *Carpinus tschonoskii*| 0.09 (±0.021) | 0.07 (±0.007) | 0.06 (±0.011) | 1.59 (±0.199) | 0.52 (±0.161) | 0.76 (±0.173) |
| *Carpinus laxiflora*  | 0.09 (±0.009) | 0.06 (±0.006) | 0.04 (±0.010) | 1.01 (±0.132) | 0.36 (±0.230) | 0.49 (±0.161) |
| Other tree species    | 0.07 (±0.005) | 0.06 (±0.003) | 0.07 (±0.005) | 1.73 (±0.072) | 0.49 (±0.093) | 0.55 (±0.082) |

Numbers in parentheses indicate standard error of the mean.
5–10 cm class and recruitment stems (2–5 cm) were continuously decreased from 2000 to 2016. However, *C. obtusa* and the other tree species showed a reversed-J pattern with multiple small stems; the peak was in the recruitment stems (2–5 cm). Other tree species and all tree stems showed a reversed-J pattern with multiple small stems, with the peak similarly in the recruitment stems (2–5 cm). The DBH size distribution of all tree stems in the GMS site showed a reversed-J pattern with multiple small stems (Figure 3(F)).

The number of dead trees, mortality rate, number of recruitment trees, and recruitment rate of dominant tree species varied according to the survey period. Annual mortality (% year\(^{-1}\)) of *Q. serrata* in each survey interval was 2.26, 3.82, and 1.23, respectively (Table 4). Annual mortality (% year\(^{-1}\)) of *C. obtusa* in each survey interval was 0.97, 1.07, and 1.82, respectively. The recruitment rate (% year\(^{-1}\)) of *C. obtusa* in each survey interval was 3.16, 3.04, and 1.60, respectively. However, the recruitment tree of *Q. serrata* did not appear during the survey period, while the recruitment tree of *C. obtusa* appeared the most.

**Discussion**

Our findings demonstrate that GMS forests are in the process of succession, moving from deciduous broadleaf forests to evergreen coniferous forests. This contrasts with typical forest succession in Korea, which usually moves from coniferous forest dominated by *P. densiflora* to deciduous broadleaf forest.

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*Figure 3.* Diameter at breast height (DBH) class distributions of the species in the permanent plot, (A) *Quercus serrata*, (B) *Chamaecyparis obtusa*, (C) *Carpinus tschonoskii*, (D) *Carpinus laxiflora*, (E): other tree species, and F: all tree stems.
dominated by *Q. serrata* (Choung and Hong 2006; Kato and Hayashi 2006). Consequently, GMS forests are composed of deciduous broadleaf species (*Q. serrata*, *C. tschonoskii*, and *C. laxiflora*) and coniferous species (*C. obtusa*) because of natural regeneration and invasion by exotic shade-tolerant coniferous species.

In 2016, the canopy of the GMS forests mostly consisted of deciduous broadleaf species (*Q. serrata*, *C. tschonoskii*, and *C. laxiflora*) while the subtree layer was evergreen conifer species (*C. obtusa*). The forest structure and dynamics were driven by differences in mortality and recruitment rates among tree species (Nakashizuka et al. 1992; Cai et al. 2020) and by the functional traits of the tree species, such as their degree of shade-tolerance (Clark and Clark 1992). The GMS forest may change from a *Q. serrata* dominated forest to a *C. obtusa* co-dominated forest because of the recruitment rate of *C. obtusa*. It is possible that recruitment of *Q. serrata* occurred but was not observed because seedling failed to survive. This could be due to the greater competitiveness of *C. obtusa*, due to its high shade tolerance (Yoshida and Kamitani 2006). Consequently, GMS forests continue to accumulate biomass despite changes in tree species composition, DBH, height, mortality, and recruitment. Generally, trees with larger DBH and height have greater biomass (Chai et al. 2019). As the major overstory tree in GMS, *Q. serrata* made an increasing contribution to total stand biomass over the 17 years of this study, due to the higher biomass accumulation of the remaining large trees with increased DBH and height. Meanwhile, *C. obtusa* as an understory tree also provided increasing stand biomass, due to an increase in the number of stems caused by a higher recruitment rate. On the other hand, the other tree species were found to have a decrease in their contribution to biomass, due to a reduction in the number of stems. The dominance of larger trees makes the forest more vulnerable to biomass losses from stochastic or disturbance-related mortality (Eisen and Plotkin 2015). Thus, it is uncertain whether biomass will continue to accumulate in GMS in the future.

Large trees are especially vulnerable to natural disturbances (Hanson and Lorimer 2007). Medium-sized trees have advantages over small and large trees in intraspecific and interspecific competition (Bastias et al. 2020). It is believed that canopy gaps in GMS forests formed by deaths of larger trees from typhoons, strong winds, or heavy rain enhance the regeneration of *C. obtusa*. Disturbances from typhoons occurred at GMS in 2002, 2003, 2007 and 2014 (Chun and Lee

| Species          | 2000–2006 | 2006–2011 | 2011–2016 | 2000–2006 | 2006–2011 | 2011–2016 | 2000–2006 | 2006–2011 | 2011–2016 | 2000–2006 | 2006–2011 | 2011–2016 |
|------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| *Quercus serrata*| 50        | 60        | 17        | 2.26      | 3.82      | 1.23      | 0         | 0         | 0         | 3.16      | 3.04      | 1.60      |
| *Chamaecyparis obtusa* | 41 | 43        | 79        | 0.97      | 1.07      | 1.82      | 142       | 128       | 69        | 3.16      | 3.04      | 1.60      |
| *Carpinus tschonoskii* | 39 | 28        | 13        | 3.80      | 4.01      | 2.18      | 2         | 0         | 2         | 0.22      | 0.36      | 0.35      |
| *Carpinus laxiflora* | 7  | 20        | 9         | 1.24      | 4.96      | 2.67      | 0         | 1         | 0         | 0.28      | 0         | 0         |
| Other tree species | 469 | 516       | 365       | 3.42      | 5.49      | 4.95      | 92        | 30        | 55        | 0.73      | 0.36      | 0.83      |
| All tree species  | 606       | 667       | 483       | 2.87      | 4.27      | 3.53      | 236       | 159       | 126       | 1.21      | 1.23      | 1.05      |

Table 4. Sequential changes in the dead tree, mortality, recruitment tree, and recruitment rate of dominant species from 2000 to 2016.
It is likely that during these years, GMS forests experienced an increase in the mortality of broadleaved species (*Q. serrata*, *C. tschonoskii*, and *C. laxiflora*), and an increase in the recruitment of *C. obtusa*. Generally, canopy gaps in climax forests are an important element in forest succession because they allow for the growth of young trees of the next generation (Jaloviar et al. 2020; Petroska 2020). In GMS forests, the mortality of *Q. serrata* in the upper layers affected the development of the middle and lower layer by increasing the opening of the canopy. Depending on the species, small trees might be more vulnerable to shade under the closed canopy or to breakage from falling stems (Miura et al. 2001). In the middle and lower layer, an increase was observed in the number of *C. obtusa* because of the change in light conditions due to the occurrence of opening caused by the damage of *Q. serrata* in the upper layer.

The direction of succession toward the climax forest composition in GMS is somewhat uncertain due to the unknown of future intensity and frequency of disturbance. The present dominant tree species, *Q. serrata*, is relatively shade-intolerant compared to *C. obtusa*, usually with only a few understory individuals (Masaki et al. 1992). *Q. serrata* can regenerate by seed dispersal only in light gaps and cannot reproduce under a closed canopy. Thus, they require gap formation for their regeneration. In contrast, *C. obtusa* is a shade-tolerant species that forms a sapling bank under a closed canopy. If disturbances are low in intensity and frequency, it will lead to a stable community structure and higher dominance of the more shade-tolerant species (Cho and Boerner 1991; Busing and White 1997).

At our study site, the numbers of *P. densiflora* continued to decrease from 40 trees ha\(^{-1}\) in 2000 to 16 trees ha\(^{-1}\) in 2016. The maximum DBH of *P. densiflora* was 40.0 cm, and the average DBH of the *P. densiflora* was 22.6 ± 1.0 cm in 2010. It is speculated that *P. densiflora* continues to decline in number because of environmental changes under climate change and competition. In addition, *P. densiflora* is vulnerable to temperature increases, and it has been reported that mortality of *P. densiflora* increases at higher temperatures (Kishi 1999). In relation to height and biomass increase, *Q. serrata* is believed to have suppressed *P. densiflora* because it exhibits a higher shade tolerance than *P. densiflora* (Beon and Bartsch 2003). Meanwhile, the BA of tree species other than the dominant species has continually declined over the 17 years of this study. This is expected to have contributed to the reduction of biomass and basal area because numbers of large-sized *P. densiflora* declined. The number of stems, basal area, and biomass of *P. densiflora* in GMS forests is expected to decrease in the future. Meanwhile, our hypothesis suggests that *P. densiflora* forests convert over time to *Q. serrata* and *C. laxiflora* forests, which is believed to be a climax forest in Korea (Park et al. 2009; Hong et al. 2012; Byeon et al. 2018). However, our results suggest that this may not be a stable forest, as exotic *C. obtusa* may be a disturbance factor in a mature *Q. serrata* and *C. laxiflora* dominated stand in GMS.

**Conclusions**

Our results indicate that the forests structure of GMS is still changing, and their live tree biomass contributes to accumulating carbon. Overall, the 17 year monitoring of the GMS forest showed that the development of the forest included increasing numbers of tree stems and increasing biomasses. Therefore, the GMS has sequestered a substantial amount of carbon through woody biomass increment and will continue to do so in the future. While *C. obtusa* was the most abundant shade-tolerant tree species in the GMS, *Q. serrata* was the dominant, relatively shade-intolerant tree species. Therefore, the forest structure of GMS is expected to continue with an increase in *C. obtusa*, while *Q. serrata* is expected to remain dominant.

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