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Relationship between the Time and Duration of Flowering in Several Woody Plants in Springtime

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ABSTRACT: To clarify the relationship between the timing and the duration of flowering among populations, plants, and individual flowers, the dates of flower budding, flowering and deflowering were monitored for ten woody species from March 1 to June 30, in 2005, 2006 and 2007, in temperate deciduous forests at three sites of Namsan, and individual plants from seven woody species were monitored from March 1 to May 31, in 2006. Total durations of flower budding, flowering, and deflowering varied among the plant species. Three durations of these phenological stages of *Stephanandra incisa* were the longest (74 days, 109 days, and 101 days, respectively), and those of *Prunus serrulata* var. *spontanea* were the shortest (7 days, 7 days, and 4 days, respectively). For each species, phenological durations varied among years but were similar among the study sites in the same year. There was no relationship between flowering time and flowering duration on the population level. On the plant level, the duration of flower budding was over 11 days in all specie; *S. incisa* had the longest duration (73.3 days), and that of *Styrax japonica* was long as well (29.0 days), while that of *Prunus leveilleana* was the shortest (11.3 days). The longer the mean flower budding duration, the greater the difference among the plants within a species. The flowering duration of for *S. incisa* was 92.2 days, while that of *Forsythia koreana* was 27.2 days. The flowering durations of all other species were 10~20 days. The deflowering duration was 92.0 days in *S. incisa* and <15 days in all other species. Differences among the plants in deflowering duration were smaller than those of the other phenological stages. In the species that flowered in April, the correlation coefficient between the flowering duration and the first flowering date was negative and significant. However, in the species that flowered in May, the correlation between flowering duration and the first flowering date was not significant. For individual plants of all species except for *S. alnifolia*, the earlier the flowering time, the longer the flowering duration. Differences between flowering time and flowering duration across years were significant in six species.

Key words: Deflowering, Flower budding, Flowering, Phenology, Springtime, Woody plants

INTRODUCTION

In annual phenological cycles, flowering phenology is particularly important because it determines reproductive synchrony with potential mates (Augspurger 1981, Marquis 1988), synchrony with or attractiveness to pollinators (Schemske 1977, Augspurger 1981, Gross and Werner 1983, Kozlowski 1992), utilization of seasonally available resources such as light or water (Schmitt 1983, Marquis 1988, Galen and Stanton 1991, Walker et al. 1995), and vulnerability to floral herbivores and seed predators (Schemske 1984, Petterson 1991, Brondy 1997, Kelly and Levin 2000, Wright and Meagher 2003). To maintain a population, the propagules such as seeds must be recruited, and seeds are produced as a result of the process of flowering, pollination, deflowering, fruit ripening and dispersal, so flowering is the first stage of recruitment in a population. Plants need to be in appropriate physiological and environmental condition to flower (Shitaka and Hirose 1998), and flowering is affected by many factors. Thus, plant flowering has been studied from many perspectives. One theme of many studies is the relationship between flowering time and its duration. These studies view flowering from the perspective of the community, the species, the population, the plant, or the flower. On a population level, previous studies have considered the plant-pollinator relationship, utilization of seasonally available resources such as water or light, production of faithful seeds, and conditions for seed germination. The results of these studies suggest that the flowering time and duration of a species evolved to be optimal to sustain its population (Primack 1987, O'Neil 1997). However, flowering times and durations are partly fixed by genetic factors but are also affected by environmental factors. Because their strategies vary across the environments experienced by the community, species, population, and plant, there is probably no simple law or principle determining a plant's flowering time and duration (Bishop and Schemske 1998).

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Many environmental factors affect flowering time and duration, but most studies have focused on the most significant factor for a given plant (Garner and Allard 1920, Flint 1974, Lieth 1974, Rathke and Lacey 1985, Diekmann 1996). For example, in tropical and arid areas with a pronounced dry season, studies have examined the relationship between flowering and water resources (Augspurger 1981, Sakai et al. 1999). In these areas, almost all plants flower within two weeks after rainfall (Marquis 1988). This result shows that water is the main factor affecting flowering times in tropical and arid area. Another study found that a plant species in an arid area flowers immediately after a fire (Arianoutsou and Mardiris 1985). In alpine or tundra, the timing of flowering is matched with the timing of snow melt, and the cumulative air temperature is the main factor (Kudo 1992, Walker et al. 1995, Thórhallsóttir 1998, Kudo and Suzuki 1999, Totland and Alatalo 2002). In temperate deciduous forests, winter is the hardest season and flowering occurs with the ascent of air temperature in springtime (Sakai et al. 1999). However, the air temperature in springtime in temperate deciduous forests does not steadily increase, but rather fluctuates by ascending above freezing and then descending again repeatedly (Min et al. 2007). In temperate areas, plants need an adaptive strategy that will allow them to maximize flowering duration as the air temperature fluctuates. Plants that come into flower early can produce better-quality seeds than those that flower late, by taking advantage of a long period for ripening and pollinator attraction (Thórhallsóttir 1998). However, if flowers flower too early, and are then faced with an abrupt drop in air temperature, the flowers might freeze and die or may not be properly timed with pollinators. Therefore, to understand how plants in temperate areas meet this challenge, studies of the relationship between flowering time and duration are needed.

The aim of this study was to clarify the relationship between flowering time and total flowering duration for several woody plants species in the early springtime in a temperate deciduous forest. We tested the hypothesis that the plants that flowered earlier had a longer flowering duration than those flowering later. We analyzed the relationship between flowering time and total flowering duration on the level of the population, the plant, and the flower.

MATERIALS AND METHODS

The study area and sites were described by Min et al. (2007). The field survey was carried out in two ways. One method involved monitoring specific populations and plants across years and sites. Ten species or plants were chosen for monitoring based on three criteria; each flowering stage was easily discriminated, plants of a species experienced the same microclimate, and there were more than three individual plants. Each phenological stage for nine plant species was monitored from February 2 to May 31 in 2005, 2006, and 2007, at three sites in Namsan. However, *Robinia pseudo-acacia* was only monitored in 2006 and 2007. Phenological stages were classified into three stages: flower budding, flowering, and deflowering. Field surveys were conducted two or three times a week.

The other method involved monitoring of flowers on plants of seven species (Table 1). Flowers on a plant were grouped by flowering date into groups of 10~30. Each flower was numbered, and its flowering and deflowering dates were determined by checking the flower two or three times a week.

Air temperature at each site was measured to the closest 0.1℃ using an automatic thermometer (LogTag, TRIX-8). The daily mean air temperature was calculated by the automatic thermometer. The year day index (YDI) and Nuttonson's index (Tn) were calculated as previously described (Min et al. 2007).

Flowering durations were calculated as the interval from the first and last flowering dates to the first and last deflowering dates for populations and individual plants, and from flowering date to deflowering date for individual flowers. Differences in the year day, year day indices and Nuttonson's indices of the first and last dates

Table 1. Species and data for flowering duration surveys

Scientific name	Month/date of flowering commencement	Period of flowering commencement
Forsythia koreana	04/05, 04/07, 04/10	03/29~04/12
Rhododendron mucronulatum	04/03, 04/10, 04/12, 04/14	04/03~04/14
Prunus serrulata var. *spontanea*	04/20, 04/24, 04/26	04/20~04/26
Euonymus sachalinensis	05/05, 05/06, 05/08	05/05~05/09
Sorbus alnifolia	05/06, 05/08	05/06~05/09
Robinia pseudo-acacia	05/22, 05/24, 06/01	05/22~06/01
Styrax japonica	05/22, 05/24, 05/26, 05/29	05/22~06/01

were calculated for each flowering stage.

RESULTS

The duration and dates of each phenological stage for varied among species and years (Table 2). However, mean flower budding and flowering durations were longer than deflowering ones. The total flower budding durations were the longest in 2006, intermediate in 2007 and the shortest in 2005 for all species except *Prunus leveilleana* and *S. alifolia*. The flower budding durations of *Forsythia*

Table 2. Date (Month/Day) of the first and last observation of each flowering phenological stage and duration (days) of phenological stages for ten woody plant species

Scientific name	Year	Flower budding			Flowering			Deflowering		
		First	Last	Duration	First	Last	Duration	First	Last	Duration
Forsythia koreana	2005	4/02	4/15	13	4/12	4/30	18	4/22	4/30	8
Forsythia koreana	2006	3/06	4/10	35	3/23	5/08	48	4/10	5/08	28
Forsythia koreana	2007	3/13	4/12	30	3/26	5/03	38	4/12	5/01	19
Rhododendron mucronulatum	2005	3/26	4/19	17	4/12	4/30	18	4/15	5/04	19
Rhododendron mucronulatum	2006	3/23	4/17	25	4/05	5/08	33	4/10	5/08	28
Rhododendron mucronulatum	2007	3/18	4/11	24	3/22	5/02	41	4/12	5/05	23
Prunus serrulata var. *spontanea*	2005	4/12	4/19	7	4/19	4/26	7	4/22	4/26	4
Prunus serrulata var. *spontanea*	2006	4/07	4/24	17	4/12	5/03	21	4/17	5/03	16
Prunus serrulata var. *spontanea*	2007	4/07	4/21	14	4/19	4/26	7	4/21	5/03	12
Prunus leveilleana	2005	4/02	4/22	20	4/19	4/30	11	4/26	4/30	4
Prunus leveilleana	2006	4/12	5/01	19	4/17	5/05	18	4/26	5/05	9
Prunus leveilleana	2007	4/12	4/26	14	4/17	4/26	9	4/23	5/03	10
Acer pseudo-sieboldianum	2005	4/22	5/10	18	4/26	5/17	21	4/30	5/17	17
Acer pseudo-sieboldianum	2006	4/17	5/13	26	4/24	5/16	22	5/05	5/16	11
Acer pseudo-sieboldianum	2007	4/19	5/07	18	4/25	5/17	22	5/07	5/18	11
Euonymus sachalinensis	2005	4/10	5/10	30	5/01	6/06	37	5/10	6/10	31
Euonymus sachalinensis	2006	4/09	5/26	47	4/29	6/03	35	5/07	6/08	30
Euonymus sachalinensis	2007	4/10	5/10	30	5/02	6/08	37	5/10	6/10	31
Sorbus alnifolia	2005	4/19	5/04	15	5/04	5/14	10	5/07	5/14	7
Sorbus alnifolia	2006	4/20	5/16	26	5/03	5/18	15	5/08	5/18	10
Sorbus alnifolia	2007	4/19	5/17	28	5/01	5/17	16	5/14	5/24	10
Stephanandra incisa	2005	4/30	5/24	24	5/24	8/30	97	6/07	8/30	84
Stephanandra incisa	2006	4/24	6/17	54	5/16	9/05	109	5/24	9/05	101
Stephanandra incisa	2007	4/23	5/28	35	5/03	8/24	113	5/10	9/01	115
Robinia pseudo-acacia	2006	5/08	5/30	22	5/16	6/20	34	5/22	6/20	28
Robinia pseudo-acacia	2007	5/01	5/25	24	5/14	6/12	29	5/21	6/18	28
Styrax japonica	2005	4/30	5/31	31	5/24	6/07	14	5/31	6/17	17
Styrax japonica	2006	4/24	6/01	38	5/16	6/20	35	5/24	6/20	27
Styrax japonica	2007	4/23	5/26	33	5/17	5/29	12	5/24	6/19	26

koreana, *Prunus serrulata* var. *spontanea* and *Stephanandra incisa* were twice as long in 2006 as in 2005. Differences in flower budding durations among the three years were largest in *S. incisa* (30 days) and smallest in *R. pseudo-acacia* (2 days). The flowering durations in most species were longest in 2006. Differences in flowering duration among the three years were largest in *F. koreana* (30 days) and smallest in *Acer pseudo-sieboldianum* (1 day). Total deflowering durations were longest in 2006 for all species except *P. leveilleana* and *A. pseudo-sieboldianum*. Differences in the deflowering duration among the three years were largest in *S. incisa* (31 days) and shortest in *E. sachalinensis* (1 day). However, despite the fact that deflowering durations were shorter than the other two phenological stages, the deflowering durations in 2006 were 3 times longer for *P. serrulata* var. *spontanea* and 2.7 times longer for *F. koreana* than those in 2005. Therefore, the durations of phenological stages were mostly longest in 2006. However, patterns of variation between years differed among species and phenological events.

On the level of the individual plant, the durations of the phenological stages did not show a trend along the species or stages (Table 3). Flower budding duration was the longest in *S. incisa* (73.3 days). Those of *E. sachalinensis*, *Sorbus alnifolia*, and *S. japonica* were also long (> 20 days). For other species, flower budding durations ranged from 11.3~18.5 days. The differences among individual plants within a species were largest in *S. incisa* (27.4 days), and were also relatively large in *F. koreana* (10.5 days). Those of the other species were relatively small (< 10 days), and the difference among plants in *R. pseudo-acacia* was only 2.3 days, despite their long flower budding duration (17.8 days). Flowering duration was longest in *S. incisa* (92.0 days) and shortest in *S. japonica* (7.0 days). Flowering durations of *F. koreana* and *E. sachalinenesis* were long (27.2 days and 24.3 days, respectively). The difference in the flowering duration among plants within a species was the largest in *S. incisa* (29.7 days), and was also large in *F. koreana* (11.3 days). Differences in flowering duration among individual plants in the other species were below 7.6 days, and that of *S. japonica* was zero among the twelve plants. The difference among plants in *E. sachalinensis* was also small (2.2 days) despite its long flowering duration (24.3 days). Deflowering durations of all species other than *S. japonica* were below 15.3 days, while the deflowering duration of *S. incisa* was 25.7 days. Differences among individual plants in deflowering duration were largest in *S. incisa* (13.6 days) and smallest in *R. pseudo-acacia* (0.7 days). The deflowering stage was the shortest of the phenological stages; however, the durations of the flower budding and flowering stages differed among species.

Correlation coefficients (CC) between flowering date (year and day) and flowering duration (days) were negative in 8 species, and significant at a 1% or a 5% level in five species (Table 4). CCs were significant in the species that flowered early in the season, before May 3, and the flowering dates were inversely proportional to flowering duration. However, in the species flowering late in the season (after May 5), there was no relationship between flowering date and flowering duration.

For individual flowers, year day (YD), YDI and Tn at the flowering and deflowering times of the seven species were as shown in Table 5. *F. koreana* and *Rhododendron mucronulatum* flowered early in the growing season, and their YDs of their first flowering

Table 3. Duration (days) of flower budding, flowering, and deflowering for individual plants in ten woody plant species

Scientific name	Flower budding	Flowering	Deflowering
Forsythia koreana	18.5±10.5	27.2±11.3	15.2± 9.5
Rhododendron mucronulatum	15.4± 6.3	19.9± 7.6	14.2± 7.2
Prunus serrulata var. *spontanea*	13.0± 3.2	14.0± 4.4	10.8± 3.1
Prunus leveilleana	11.3± 3.7	11.0± 2.9	8.0± 2.4
Acer pseudo-sieboldianum	18.4± 7.1	14.9± 7.3	7.0± 2.8
Euonymus sachalinensis	23.3± 3.1	24.3± 2.2	15.3± 4.8
Sorbus alnifolia	20.3± 2.9	12.3± 1.8	10.3± 1.5
Stephanandra incisa	73.3±27.4	92.0±29.7	25.7±13.6
Robinia pseudo-acacia	17.8± 2.3	14.5± 6.3	9.7± 0.7
Styrax japonica	29.0± 8.5	7.0± 0.0	15.0± 8.7

Table 4. Correlation coefficient between flowering time (date, YD) and flowering duration (day) in 10 woody species

Scientific name	Mean flowering date	CC value (*n*)	Significant level
Forsythia koreana	April 4	−0.965 (9)	0.01
Rhododendron mucronulatum	April 9	−0.841 (17)	0.01
Prunus serrulata var. *spontanea*	April 15	−0.852 (11)	0.01
Prunus leveilleana	April 20	−0.528 (11)	-
Acer pseudo-sieboldianum	April 28	−0.588 (15)	0.05
Euonymus sachalinensis	May 3	−0.801 (9)	0.05
Sorbus alnifolia	May 5	−0.518 (13)	-
Stephanandra incisa	May 17	−0.396 (8)	-
Robina pseudo-acacia	May 20	0.190 (12)	-
Styrax japonica	May 22	0.113 (17)	-

Table 5. YD, YDI and Tn at the times of flowering and deflowering in seven woody species

Scientific name	Flowering time			Deflowering time		
	YD	YDI (℃ · day)	Tn (℃ · day)	YD	YDI (℃ · day)	Tn (℃ · day)
Forsythia koreana	95	276.0	75.7	119	541.8	228.9
Forsythia koreana	97	294.7	85.8	120	557.0	239.2
Forsythia koreana	100	332.0	109.8	114	481.1	191.5
Rhododendron mucronulatum	93	252.7	62.9	108	426.2	164.3
Rhododendron mucronulatum	100	332.0	109.8	113	471.5	185.7
Rhododendron mucronulatum	102	363.0	130.6	115	492.1	197.7
Rhododendron mucronulatum	104	384.0	141.8	115	492.1	197.7
Prunus serrulata var. *spontanea*	110	440.8	169.3	115	492.1	197.7
Prunus serrulata var. *spontanea*	114	481.1	191.5	118	528.3	219.8
Prunus serrulata var. *spontanea*	116	503.9	204.7	119	541.8	228.9
Euonymus sachalinensis	125	642.9	301.1	130	731.6	367.5
Euonymus sachalinensis	126	657.4	310.5	130	731.6	367.5
Euonymus sachalinensis	128	694.3	339.2	132	764.9	391.6
Sorbus alnifolia	126	657.4	310.5	128	694.3	339.2
Sorbus alnifolia	128	694.3	339.2	132	764.9	391.6
Robina pseudo-acacia	142	938.8	521.7	147	1,022.4	583.9
Robina pseudo-acacia	144	969.6	544.4	151	1,143.4	657.1
Robina pseudo-acacia	152	1,143.4	657.1	154	1,186.4	695.0
Styrax japonica	142	938.8	521.7	148	1,037.8	595.2
Styrax japonica	144	969.6	544.4	149	1,054.7	608.2
Styrax japonica	146	1,006.6	573.1	150	1,073.8	573.2
Styrax japonica	149	1,054.7	608.2	152	1,143.4	657.1

were in the range of 95～100 and 93～100, respectively. However, *R. pseudo-acacia* and *S. japonica* flowered late in the growing season, and their YDs of their first flowering were 142～152 and 142～152, respectively. YDs at deflowering time were low (108～115) in *R. mucronulatum*, intermediate in *P. serrulata* var. *spontanea* (142～152) and the largest in *R. pseudo-acacia* (147～154). That of *S. japonica* was also relatively large (148～152). YDs differences between the first and the last flowering times were larger than those for deflowering times. YDs differences between the first and the last flowering time were the largest in *F. koreana* (14 days) and the smallest in *S. alnifolia* (3 days). Differences in YDIs between the first and the last flowering times were below 50℃ · day in *S. alnifolia*, but over 100℃ · day in *R. mucronulatum*, *P. pseudo-acacia*, and *S. japonica*. However, those between the first and the last deflowering times were below 50℃ · day in *P. serrulata* var. *spontanea*, and *E. sachalinensis*, but over 100℃ · day in *R. pseudo-acacia* and *S. japonica*. Differences in Tns between the first and the last flowering times were below 50℃ · day in *F. koreana, P. serrulata* var. *spontanea, E. sachalinensis,* and *S. alnifolia*, and over 100 ℃ · day in *R. mucronulatum* and *R. pseudo-acacia*. Tns differences between the first and the last deflowering times were below 50 ℃ · day in *F. koreana, R. mucronulatum, P. serrulata* var. *spontanea, E. sachalinensis* and *S. alnifolia*, and over 100℃ · day in *R. pseudo-acacia*.

Correlations between YD, YDI, and Tns for flowering duration and flowering times for a species were significant at 1% or a 5% level along the species (Table 6). In general, the earlier the flowering time, the longer the flowering duration. Moreover, differences

Table 6. Differences of YD, YDI and Tn between the flowering time and the deflowering time in seven woody species

Scientific name	YD	Indices					
		YD (day)		YDI (℃ · day)		Tn (℃ · day)	
		D*	SL** (%)	D	SL (%)	D	SL (%)
Forsythia koreana	95	24.2±2.8	a(1)	274±41	a(1)	157±25	a(1)
Forsythia koreana	97	22.9±2.4	a(1)	260±35	a(1)	145±21	a(1)
Forsythia koreana	100	14.1±3.7	b(1)	140±42	b(1)	79±22	b(1)
Rhododendron mucronulatum	93	15.1±6.0	a	165±62	a(1)	93±32	a(5)
Rhododendron mucronulatum	100	13.0±5.6	a	130±64	b(5)	75±34	ab
Rhododendron mucronulatum	102	12.5±4.0	a	131±53	b(5)	67±29	ab
Rhododendron mucronulatum	104	11.2±5.1	a	109±64	b(1)	59±34	b(5)
Prunus serrulata var. *spontanea*	110	5.4±1.9	a(5)	49±24	a	26±13	a
Prunus serrulata var. *spontanea*	114	3.9±1.7	b(5)	37±23	a	20±13	a
Prunus serrulata var. *spontanea*	116	3.3±1.2	b(5)	32±17	a	19±10	a
Euonymus sachalinensis	125	5.5±1.5	a(5)	84±27	a(5)	58±21	a(1)
Euonymus sachalinensis	126	4.3±1.5	ab	62±28	ab	46±22	ab
Euonymus sachalinensis	128	3.8±1.6	b(5)	49±24	b(5)	38±19	b(1)
Sorbus alnifolia	126	2.0±0.0	a(1)	20± 0	a(1)	14± 0	a(1)
Sorbus alnifolia	128	3.9±1.4	b(1)	52±22	b(1)	41±16	b(1)
Robinia pseudo-acacia	142	7.0±0.0	a(1)	107± 0	a(1)	74± 0	a(1)
Robinia pseudo-acacia	144	6.6±1.5	a(1)	105±30	a(1)	74±23	a(1)
Robinia pseudo-acacia	152	2.0±0.0	b(1)	23± 0	b(1)	20± 0	b(1)
Styrax japonica	142	6.0±1.7	a(1)	90±29	a(5)	61±22	a(5)
Styrax japonica	144	5.0±0.0	a(1)	71± 0	ab	51± 0	ab
Styrax japonica	146	4.1±1.5	ab	58±32	ab	38±22	ab
Styrax japonica	149	3.4±0.8	b(1)	52±20	b(5)	38±15	b(5)

* difference, ** significant level (%).

in flowering duration and the three indices among the years were significant at a 1% level in two species (*F. koreana* and *R. pseudo-acacia*) and significant at the 5% level for all other species except for *R. mucronulatum* and *P. serrulata* var. *spontanea*.

DISCUSSION

The times of flower budding, flowering, and deflowering varied among populations and years. This is probably due to differences in air temperature regimes between two of the study years (Min et al. 2007). The period with air temperature below 0℃ in March was longer in 2006 than in 2005, but, after mid-April, the air temperature or YDI or Tn was higher in 2006 than 2005 (Min et al. 2007). However, the flowering order was constant among the species for two years. The earlier the phenological stage, the greater the difference between the first and the last times for a species or a stage. Generally, within-population flowering order remained approximately constant between years, despite differences in the dates of the population flowering periods. This result suggests that the timing of an individual's flowering is largely determined by relatively fixed characteristics of its microhabitat or genetic factors or both (Buide et al. 2002).

In an individual level, two patterns emerged from the field survey data. The deflowering duration was consistently shorter than the flower budding and flowering durations. However, the flower budding duration could be longer or shorter than the flowering duration. The longer the duration of a phenological stage, the greater the variation in duration among the plants. In addition, the earlier the date of flowering, the longer the flowering duration. The correlation coefficients between flowering time (YD) and flowering duration were negative and significant at the 1% level in the species that flowered before mid-April, and correlations for the species which flowered by early May were negative and significant at the a 5% level. However, in the species that flowered after this time, there was no relationship between flowering time and flowering duration. Therefore, low temperatures in the springtime prolonged the flowering duration. Plants that start flowering early tended to have longer flowering periods than plants that start flowering late, as has been reported in many previous studies (Dieringer 1991, Kelly 1992, O'Neil 1997, Buide et al. 2002).

On the level of the individual flower, the earlier flowering occurred, the longer the flowering duration for all species except *S. alnifolia*. Species that flowered in early May showed a negative relationship between flowering time and flowering duration, although populations and individual plants did not. That was, the flowers of a plant had a similar deflowering time regardless of their flowering time.

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